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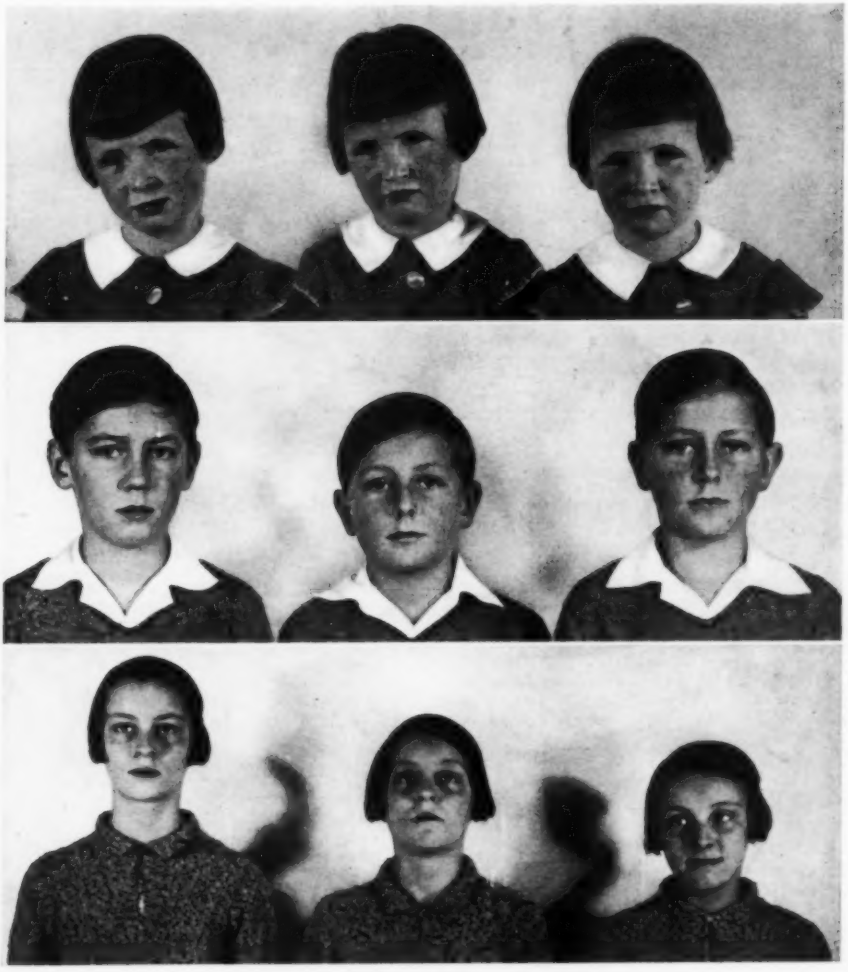

THREE KINDS OF TRIPLETS

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The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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The

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DEGENERATION OF CACAO THROUGH HYBRIDIZATION

Frontispiece

In years gone by the Criollo Cacao of Venezuela (*Theobroma cacao*), was famed for its excellence. This form is represented in the photograph by the type of pod shown at the lower right. This species is not as productive as a species native to Trinidad (*Th. leiocarpa*), the type of which is shown at the upper left. As a consequence, about a century ago the Trinidad cacao was introduced into Venezuela. Since that time natural hybridization has taken place so that at present a great variety of forms is being produced. The 28 pods shown here are each typical of an individual tree. This has resulted in the rapid deterioration of Venezuelan cacao, so that at present it is almost worthless because the seeds are so variable in constitution that they cannot be processed satisfactorily.

DEGENERATION OF CACAO THROUGH NATURAL HYBRIDIZATION

H. Pittier
Caracas, Venezuela

THROUGHOUT the Spanish colonial epoch and for many years after Venezuela had gained its independence, the native cacao was famed for its excellence. The cacao plantations scattered along the seaboard were entirely of the *criollo* variety, corresponding to what is still considered as the typical *Theobroma cacao* of Linnaeus. As the trees of wild cacao scattered in the primaeval forests of the Upper Orinoco, in the Guayanas and perhaps along the foot of the Andes, apparently all belong to the other extensively cultivated species, *Th. leiocarpa* Bernouilli, it has been inferred that the Venezuelan *criollo* was originally imported from Central America where it has been cultivated since time immemorial.

Such at least was the opinion of my friend and very learned colleague, the late Dr. Lisandro Alvarado, who cited in support of this belief a historical document attributing to the Franciscan monks and missionaries the introduction of cacao into Venezuela. Alamo[1] also states that the first plantations in the State of Miranda in Venezuela were established by Aragonese Capuchin friars, who brought the seeds either from Nicoya in Costa Rica or from Cuba. He adds that these first plantations were located in the lands of Curiepe and Cūpira in the Barlovento region of Miranda and that they were rapidly extended until cacao became one of the main export products of the country. The same origin can probably be claimed for the famed plantation of Chuao, hidden in an isolated valley of the northern slope of the Coast Range, where the same Franciscan or Capuchin Fathers had founded a settlement with fugitive negro slaves.

On the other hand, the noted local historian Tulio Febres Cordero, in an interesting contribution to the history of the primitive inhabitants of the Venezuelan Andes[4], explains that a cacao of excellent quality was cultivated in Mérida before the Conquest and that its beans were used in the preparation of a drink called *chorote*, in every way similar to the Mexican chocolate. In the same paper, it is also stated that wild cacao trees existed, forming "immense groves," besides those cultivated in extensive plantations of the then Gobernación de Mérida, by Jesuit missionaries. According to the same author, the tree is still growing wild in the virgin forests of the region, an assertion which it would be very interesting to verify.

The cultivation of *Th. leiocarpum* Bernouilli, or *calabacillo*, is apparently of much more recent origin. It began with the advent of the first European immigrants in the Lesser West Indies and in the Guayanas, whence it was propagated as far as Jamaica, where it may have met with *Th. cacao*, coming from Yucatan through Cuba and Santo Domingo. That cacao had very little economic importance among the aborigines of eastern South America is shown by the fact that there are only a few names in the native vocabularies and that the so-called "Lingua Geral" used the term *cacañ*, derived from the Nahuatl language.

De Candolle, in his "Origine des Plantes cultivées,"[3] is not very explicit concerning cacao. When his book was first written, very few botanists admitted the distinction already established by Bernouilli[2] between the several cultivated species. All grades and varieties were still included under *Theobroma cacao* L. and even today

typical of an individual tree. This has resulted in the rapid deterioration of Venezuelan cacao, so that at present it is almost worthless because the seeds are so variable in constitution that they cannot be processed satisfactorily.

very few among those who have written on the culture of this plant seem to have a clear idea of the specific characters by which the several types are distinguished.*

For any botanist who, like myself, has had opportunities to observe cacao trees in wild condition, there can be no doubt as to the specific validity of *Th. leiocarpum*. The third cultivated species, *Th. pentagonum*, has not been reported so far outside of plantations, but is equally well characterized.

Unfortunately, I have never collected the two first species when I found them in places where the interference of man could not be suspected. I have observed colonies of *Th. leiocarpum* in Costa Rica, Panama and in the virgin forests of the west of Lake Maracaibo. It is also frequently mentioned as growing in the forests of the Guayanas and in the Amazon basin. *Th. cacao* has been seen growing in the northern parts of Central America, on the Atlantic watershed of Costa Rica, in the region around Bocas del Toro and in Southern Darien in Panama, but there is no well founded report of it in wild condition farther East, though, as we have seen, there is a remote possibility of this species being indigenous in some parts of the Venezuelan Andes. Several other travellers have reported the existence of wild cacao trees, but they are never explicit as to the species.

In a general way, it may be concluded from the information at hand, that *Theobroma cacao* in its wild condition is found in Central America and the northwestern part of South America, and *Th. leiocarpum* is indigenous all over the northeastern part of South America and extending far into Central America. *Th. pentagonum* is found only in a restricted area, including Nicaragua and perhaps part of Costa Rica, extending north to the southern border of Guatemala.

It is difficult to identify the species of cultivated Theobroma from herbarium specimens. These are usually labelled *Th. cacao* L. and in most cases originate from plantations, so that their specific purity is almost always doubtful. An added difficulty arises from the fact that the available specimens of cacao in flower very rarely are accompanied by specimens of fruits or seeds. These are almost indispensable for an accurate classification of these plants in the light of present knowledge. It is very likely that some of Bernouilli's new species have been described from cultivated specimens and even the Jamaican type of *Theobroma cacao* L. may be a hybrid, since it is not improbable that both *criollo* and *calabacillo* existed in that island at the time when the specimens upon which Linnaeus founded his species were forwarded to him. The detailed descriptions and, above all, the illustrations found in the works of Browne and others do not correspond at all closely to the criollo cacao as we know it in its wild condition or in the plantations of northern Central America.

Another difficulty is due to the fact that most botanists who have worked on the genus had never seen uncultivated cacao trees or even a cacao plantation and so could not realize the striking differences existing in the specific characters of these plants. Thus Schumann, in his treatment of the genus Theobroma in *Flora brasiliensis*, simply included the whole group of cultivated cacao trees under *Th. cacao* and treated as simple varieties several of the species created by Bernouilli.

In addition to the taxonomic problems brought about by the utilization of two or more species of this plant, their distribution by man has given rise to a practical problem of great interest and of no little importance to a whole region of Venezuela. I now propose to show that as a result of the

* Thus van Hall in his (in all other respects) excellent treatise on cacao and its culture (*Cacao*, by Dr. C. J. J. van Hall, Director of the Institute for Plant Diseases and Cultures, Buitenzorg, Java—London 1914) falls in a double error when he cites *Th. cacao* and *Th. pentagonum* as the two species producing the cacao of commerce. In the first place, the latter has no commercial importance, and secondly it cannot be confused with *Th. leiocarpum*.

interplanting of two distinct species, degeneration of cacao as a commercial product has come about. As explained above, the criollo cacao was originally the only variety under cultivation in that country and, owing to its superior quality, this cacao enjoyed a well deserved preference.

About 1825, the so called *trinitario* cacao was introduced from Trinidad to a plantation located along Rio Guapo, not far from the town of Rio Chico. This variety belongs to a group of forms derived from, or akin to, the calabacillo, *Theobroma leiocarpum* Bern. In a letter reproduced in the first (and only) volume of proceedings published by the Sociedad de los Amigos del Pais, a cacao farmer, who signs only the initials J. R. de M., describes the first stages of this experiment, as compared with the planting and growth of the criollo cacao. This writer concludes from his observations that the trinitario has but a slight advantage over the criollo and that its cultivation should be abandoned. Notwithstanding an energetic protest from the above named society, no measures were ever taken to check the propagation of the inferior variety and its planting continued on an increasingly large scale. Thus began the ruin of the Barlovento cacao plantations. Henceforward, the two species, *Theobroma cacao* L. and *Th. leiocarpum* Bernouilli, were both propagated throughout the region. We will now see what were their reciprocal reactions. It will, however, help us in this if we first acquire a better knowledge of their characters and peculiarities.

There are no outstanding differences which make it easy to distinguish the trees of the two species. Both have the same mode of growth, producing first a straight shaft and then a whorl of three to five horizontal branches. After these have acquired a certain development, a bud appears directly below their insertion and grows vertically, further extending the stem until a new whorl of primary branches is formed, this process being repeated indefinitely. In the plantations, however, this mode of growth is seen only on young trees, for later on lateral branches alone are allowed to stand so that the original, pyramidal form is lost.

There is a difference in the size of the leaves, those of *Th. leiocarpum* being slightly larger. The workmen in the plantations can readily tell a criollo tree from a trinitario even from a distance. This I have never been able to do and, at first sight at least, there is no apparent difference in the flowers. According to Bernouilli, the pedicels are glandulous-pilose in *Th. cacao* and *Th. pentagonum* and covered with sessile glands in *Th. leiocarpum*, while the blade of the ligula is rhomboid, acuminate and subcrenate toward the apex in *Th. cacao* and *Th. leiocarpum*, and broadly obovate or subtriangular-truncate at the apex, which is sometimes mucronulate, in *Th. pentagonum*. The same author adds that in the latter species, the size of the flowers is only about half that of those in *Th. cacao*.

The fruit and seeds show the most characteristic and striking differences. In the pure strains of *Th. leiocarpum* as found wild, the fruit is ovoid, broadly obtuse at both ends, with a smooth, greenish or more or less pink or purple surface, the sutures of the carpels being indicated by five broad, shallow grooves. The exact dimensions have never been accurately ascertained, but I would say from memory that ripe fruits are about ten cm. long, with a diameter of six to seven cm. It is noteworthy that much smaller fruits are seen in the plantations on the receding forms called *cacao macho* and *cojón de toro;* one of these, fully mature, was found to be 8.7 cm. long and 5.2 cm. in diameter. The seeds are small, flat and more or less triangular; when cut across, the cotyledons show an intense purple coloration and their taste is bitter, due seemingly to their richness in tannic compounds. It may be recalled here that, as also in

the two other species under consideration, these seeds are attached to a central placenta, in two longitudinal rows of six to ten in each cell, and in the mature fruit the walls of the cells and other dissepiments resolve themselves into a fleshy, soft, sweet pulp.

The typical fruit of *Th. cacao* is quite distinct in shape from that of *Th. leiocarpum*. It is more elongated, obtuse at the base but decidedly acuminate at the apex, which is obtuse and more or less curved. The surface of the pod is verrucose and, besides the grooves marking the carpel sutures, which are deeper and narrower than in *Th. leiocarpum*, there are five additional, shallow grooves, dividing each valve in two longitudinal halves. The color of the pods varies from apple-green to yellow, pink, or dark purple. The seeds are cylindrical, rounded at the ends and, when cross-sectioned, the cotyledons are seen to be of a pale yellow color; as to taste they are perfectly insipid.

In *Th. pentagonum*, we have another characteristic feature in the salient suture of the carpels, in the shape of narrow ridges, alternating with five dorsal, shallow grooves. The general shape and color of the pod are the same as in *Th. cacao* and the seeds show identical characters, though they are said to be on the average a little larger than in the latter species.

Before going further, it may be added that *Th. bicolor* H. & B. and *Th. angustifolium* Moc. & Sessé, which have often been mentioned as being cultivated and which are specifically very distinct from the species just described, sometimes are found in plantations but are never propagated. These plants usually represent remnants of the primitive forests which occupied the soil prior to cultivation. *Th. bicolor* is characterized mainly by the hard, nut-like shell of its pods, *Th. angustifolium* by its yellow flowers.

We now come again to the introduction of the *cacao trinitario* or *calabacillo* in Venezuela and its rapid spread in all the plantations of the Barlovento region. In spite of warnings and protests, trinitario soon became the much more popular variety and many advantages were claimed for it. The trees were far more robust than were the criollo trees. Their growth was more rapid, they began to produce much sooner and the returns were more abundant. As the first signs of cross-fertilization appeared, it was even claimed that the qualities of trinitario were improved by planting in the rich alluvial soils of Barlovento, an idea which is still widely prevalent.

If the crossing had gone on only between the original parents the result might have been an intermediary variety akin to the *forastero* of the Island of Trinidad, and this could have been maintained by a careful selection of the seeds and better cultivation. But the plants were practically left to their fate and the propagation and replanting has been carried on as has always been the practice, not only with cacao but also with coffee, simply by means of natural seedlings, picked up from under the old trees. Thus the hybridization process was allowed to continue unhindered, not only between the original species but between the hybrids of the first and later generations. This has resulted in an endless variety of forms, producing more and more heterogeneous cacao beans, and consequently worse and worse grades of commercial cacao. Today the quality of the Barlovento cacao has declined to such a low point that it is hardly fit for the market.

On my first visit to the plantations of Barlovento in 1913, I was struck by the predominance of forms nearly related to the typical calabacillo. Since then this relationship has become more and more evident. Not only the shape of the pods, but also the purple coloring of the cotyledons (found even in pods which in external appearance closely resembled the criollo) shows the effects of the inferior type. An intelligent planter gave me the key to this situation when he said: "One calabacillo tree in a plantation of *cacao dulce*

(criollo) is sufficient to spoil in time the whole plantation, but one single tree of criollo has no visible action on a plantation of trinitario."

That is to say, the more primitive form, the cacao calabacillo, shows a distinct tendency to be dominant, and its pollen completely masks many criollo characteristics in the hybrid. That differential pollen viability may also be a factor in favor of the wild type is indicated by an experiment I made in order to get information on this point. The results are admittedly far from conclusive because of the unfavorable conditions under which they were made, but so striking and so well in accordance with the above expressed opinion of a practical farmer, that I wish to mention them, if only to induce other observers to repeat and verify them. Some fifteen grains of pollen taken from flowers brought from Hacienda Chuao and purported to be pure criollo, were placed in a solution of 30 per cent sugar in pure water. After two hours and forty-five minutes only six pollen grains had germinated. A second experiment was made with pollen of *cojón de toro*, a degenerate form very similar to the typical *Th. leiocarpum*. Thirteen grains were counted in the field of the microscope and in an hour and a half twelve of them had developed a tube. I repeat that these experiments were not made under strictly adequate conditions and that they should be repeated on a larger scale. Nevertheless, they point to the fact that pollen growth appears to be much more active in the strains more nearly related to *Th. leiocarpum*. If we remember first, that the cultivation of *Th. leiocarpum* is comparatively very recent, and secondly, that in some plants cultivated since the beginnings of civilization there is a marked tendency toward sterility, we realize why the pollen of criollo cacao is less viable than that of calabacillo. In support of this view it may be added that pure stands of criollo cacao are never heavy producers.

In order to give an idea of the extraordinary intermixing of the two species, *Th. cacao* and *Th. leiocarpum*, I have brought together twenty-eight of the forms observed in the plantations of Barlovento, and placed them in accordance with their probable relationship (Frontispiece). The pod at the upper left corner is the form which is fast disappearing, known as *cacao macho*, supposed to be closely related to the typical *Th. leiocarpum*. That at the lower right is very close to *Th. cacao*.

Much the same transition is observed in the seeds, with the exception that even in the pods more nearly like those of the typical criollo, thin purple threads were noticed in the cotyledons. It is also worth recording that, though in most of the pods the coloring of the beans is uniform, in some cases a few are dark purple, and others a lighter color, indicating fertilization by pollen of two different plants. We may add that the twenty-eight variations shown in Frontispiece, are by no means all of those observed. In 1913 I listed sixty-four distinct shapes of pods.

Cacao is not a product that goes directly from the field to the market. Before being dried and bagged it has to be submitted to a delicate process of fermentation, one of the main objects of which seems to be the elimination of the bitter substances contained in the bean. These substances scarcely exist in the seeds of criollo cacao, while they are abundant in the calabacillo. Hence the fermentation process is very short in the first case, while it may last for two or three days in the latter. For correct fermentation it is necessary to have a homogeneous bean mass. Inferior classes of cacao of a pure race can always be turned into a commercial product by a well calculated fermentation, but this is not possible in the case of a heterogeneous mixture such as the one just described. If the beans are kept too long in the fermentation boxes, those which are nearer to *Th. cacao* will be spoiled and transformed into an amorphous substance, deprived of its essential oil and of theobromin. With a short fermentation,

the larger number of beans remain "half cooked" and partially useless.

I have seen lately several reports on Barlovento cacao samples, written by expert brokers of France and England, and they all agree in describing them as unfit and scarcely salable. So it has become more and more evident that, if prompt and energetic measures are not taken, the product of the whole Barlovento region will be eliminated from the market. The only practical way to rehabilitate the affected plantations would be, it seems, to gradually eliminate the inferior varieties and substitute for them trees of the best strains. As this measure would have no effect unless general, it would have to be made compulsory by law and executed at the same time, under official supervision, over all the plantations of the affected district.

A large number of instances might be cited in which plant hybridization has produced very beneficial results. Why is it that in the case of the Barlovento cacao the effects have been so disastrous? The reason for this is not far to seek. In cases where hybridization has proved beneficial, selection in some form has probably always been used to cull out the economically undesirable variants, or asexual propagation has been resorted to to perpetuate the more desirable forms. Reference has been made in the JOURNAL in previous years to the effects in cotton[3a] of a policy of uncontrolled hybridization. The situation in the cacao plantations of Venezuela is a striking parallel to this, but in an aggravated form, in that hybridization has been between two distinct species rather than between varieties. Since random selection of seedling plants for propagation purposes has been practiced the situation has been about as bad as it could be. Thus it is seen that the plight in which the cacao planters of the Barlovento region find themselves is not an exception to known biological laws but rather a demonstration of the need for application of recognized principles of plant breeding. If these are not soon put into practice, the errors of the past will inevitably result in the destruction of an ancient agricultural industry in the region in question. Even now it is in the last stages of demoralization through failure to heed the warnings sounded over a century ago when this tragic "experiment" was short sightedly undertaken.

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◆

Getting Acquainted with the Wild Flowers

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HIRAM M. SHOWALTER
The Blandy Experimental Farm

*HOUSE, HOMER D., *Wild Flowers.* Pages, 362. Price, $7.50. The Macmillan Company, 1934.

THE RADIOLOGICAL EXAMINATION OF THE SKELETONS OF TRIPLETS

FRANZ BUSCHKE*

THE present report deals with the results of a detailed radiological investigation of five sets of triplets, ranging from four and a half to twelve years in age. In a report of a similar study of twins this material was mentioned but it is here proposed to present a detailed examination of the material.

Triplets are not a common occurrence. Hellin's formula postulates twins to every eighty single births and triplets to every 80^2, that is, one set of triplets in 6,400 single births. Bumm's[3] examination of the statistics on triplet births confirmed this expectation. By no means all triplets survive birth and infancy and thus, in the population at large the occurrence of triplets is even more rare. The very infrequency is a justification of this report, but the further and more important justification is that it is possible to confirm the results of similar observations on twins.

In recent years the most prolific source for data to explain the mechanism of human inheritance has been the material derived from the study of twins. The results of such investigations, especially those dealing with identical twins reared apart, facilitate the separation and evaluation of the effects of hereditary and environmental factors. The skeletal development of these triplets will be studied from this point of view. An effort will be made to distinguish between the influence of heredity and environment. Each trio has grown up, as far as this is humanly possible, under the same environmental conditions. It is true that all members of a trio have the same father and mother, but the modern conception of the Mendelian mechanism of heredity shows that such groups need not have an identical genetic constitution. Both among triplets and among twins we find partners who possess the same gene material and partners possessing different genes. In the case of triplets the following combinations are possible:

1. All three possess *identical* material.
2. All three possess *different* material.
3. Two possess the *same*, and the third a *different* gene-complex.

The investigation of the similarity among members of a trio is the deciding factor in the determination of the group to which they belong. Those of group 1, *genotypically identical*, are almost always characterized by startling similarity in all observable respects. We can hardly imagine that three individuals could be so much alike in so many characteristics, which must depend for their expression on the action of a great number of different genes, unless these individuals originated from the same chromosome mass. The chance occurrence of such absolute identity of chromosome material in two separate zygotes is highly improbable and in three zygotes is unthinkable. All three partners of a trio showing this almost ridiculous similarity must be regarded as having developed from a single zygote—through the process of *Polyembryony*. Examples of Polyembryony are found in other animal species, e.g. the armadillo (Newman and Patterson).

The mechanism involved in the production of a trio showing no particular similarity in the sense that we have used it above is clear. Each partner

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has a different gene-complex, and has therefore different chromosome material and must have developed from a separate zygote. Three separate ova have in such case been fertilized simultaneously by three sperms, and three zygotes have developed by *Polyovulation*. The genetic relationship of such triplets is equivalent to that of ordinary brothers and sisters.

The mechanism involved in the production of triplets of the third group is not at present known for certain. It is generally accepted that a combination of polyovulation and polyembryony occurs—one zygote develops twins and another zyogte develops a single foetus. Other possibilities are indicated by the phenomenon of inheritance of the tendency to bear twins. Curtius has developed an hypothesis which I have discussed in detail elsewhere.[5]

The causal mechanism involved in the production of a trio two of whose members possess identical, and the third different chromosome material is, in this paper, secondary to the question of the relative influence of heredity and environment in the skeletal development. It is however important to realize the existence of, and the sharp distinction between, these three categories of triplets.*

Diagnosis of Identical Triplets

At one time the differential diagnosis of the three classes of triplets was made from a consideration of the chorion. Gynecologists were particularly inclined to regard the arrangement of the chorion as decisive. Corresponding to the fact that Class I (UT) triplets develop from one zygote there should be one chorion (monochoric triplets). On the other hand triplets developing from different zygotes (Classes II [BT] and III [TT]) should possess different chorria. This is usually the case. Twins or triplets that have developed from different zygotes lie in different choria (provided the partition wall has not disappeared during the process of development[1]). Under these circumstances traces of the common wall are usually to be found.[10] Twins or triplets that have developed from one zygote have almost invariably a common chorion, but the investigations of Siemens, Curtius and Lassen and of von Verschuer have shown that twins which, in view of the results of the investigation of their similarity, must be regarded as uniovular, can nevertheless develop in separate choria. Among 14 pairs of twins which similarity tests demonstrated with a high degree of probability to be uniovular, Curtius and Lassen found no less than five pairs of dichoric twins. The chorion arrangement is evidently in no sense decisive evidence. It is clear that the development of the choria in the case of uniovular multiple births depends on the moment at which the twins or triplets begin to manifest themselves in the developmental process. Should this manifestation occur after the differentiation of the fertilized ovum into embryoblast and trophoblast has taken place, (this means at the stage of the blastula), then but a single chorion will develop and the polyembryony will

*Corresponding to the literature on this subject we shall adopt the following nomenclature:

1. Uniovular triplets (UT) (Class I).
2. Biovular triplets (BT) (Class II).
3. Triovular triplets (TT) (Class III).

Concordant, concordance=Close similarity or identity with regard to a particular phaenotypic characteristic among individuals under discussion.

Discordant, discordance=Dissimilarity with regard to such characteristic.

This nomenclature permits the following summary:

Uniovular (Class I) triplets show concordance of the characteristics selected for the determination of the group.

Biovular (Class II) triplets are composed of two concordant partners, the third is discordant.

Triovular (Class III) triplets are all discordant.

This nomenclature conforms to the observed facts, and may be utilized even though we must still theorize over the mechanism of the production of triplets.

proceed through a polycentric development of the embryoblast. Should polyembryony manifest itself before the blastula stage is reached, then the trophoblast will develop a corresponding number of choria with the resultant polychoric multiple birth of infants with identical chromosome material.

The amnion appears at a later stage and the development of one or more amnia depends on the extent to which the embryonal disks develop in association.[3]

Frequency of Three Types

With regard to the frequency of the various types, it is difficult to analyze the earlier literature. Most authors are agreed that dichoric—reported as "biovular"—triplets are most frequent, followed by the trichoric—"triovular" —whereas the monochoric—"uniovular" —are the least common. Saniter[18] found in 30 cases of triplets two choria 14 times, three choria 9 times and one chorion but twice. It is clear from what has already been said, that some of the trichoric—"triovular" (Class III) triplets could probably, as a result of the investigation of their similarity, have been shown to be genetically uniovular. Saniter[18] found that both the monochoric and trichoric triplets always had three amnia. He does not give details with regard to the dichoric triplets. Durieux[10] reports a case of three foetuses in one amnion. In both cases from Robert Meyer[16] of monochoric triplets there were three amnia. In one of the cases that we are describing below which, as a result of the similarity investigation, is most certainly to be regarded as uniovular, there were three amnia. Uthmoller[20] reports a case of dichoric triplets with two amnia which corresponds exactly to a case of mine of biovular triplets, which is reported below.

We see that Class I triplets are usually monochoric with three amnia, Class III are trichoric with three amnia, whereas the data concerning Class II are uncertain. It is probable that Class II are biamniotic. In our Class II cases, the two foetuses shown to possess the same chromosome material lay in one amnion, whereas the third had a separate amnion of its own.

In the more recent literature the differential diagnosis of the three classes of triplets has always been made from the similarity investigation. Von Verschuer[21] reports female Class I (UT) triplets in which the identity of the chromosome material is obvious from the photographs. Clarke and Revell[8] demonstrated three sets of Class I (UT), one female, one male (10 years old) and one male (17 months). In the last case the chorion arrangement was known: The triplets had developed from one placenta and in one chorion. The amnion was not reported. In this case the triplets were concordant with regard to their lefthandedness, a character that they had inherited from their mother. In another case two of the partners were lefthanded and the third righthanded. This does not however disprove the diagnosis, for we know from the results of investigations of asymmetry in twins that handedness is not decisive. Further, Clarke[7] in 1932 reported a set of monochoric female quadruplets. As a result of the investigation of their similarity (e.g. the skin folds of the hand) the diagnosis of uniovular quadruplets was possible. Hartmann [14] described a case of Class I triplets in which he had examined the skeleton. This case was originally reported by Robert Meyer. I have not been able to find any other case of triplets in the literature in which radiological examinations have been made, and a summary of Meyer's findings is therefore presented:

It was a case of monochoric triamniotic male triplets. The fact that they had a common chorion must be regarded as evidence, though not decisive, that they belonged to Class I. The investigation of similarity was impossible in newly born infants. The first child was normally developed, 52 cm. in length and 3,000 gms. in weight. The placenta was hyperæmic, the child was born dead. The second child was born alive and lived. It was 45 cm. long, 2,400 gm. in weight, the placenta was more normal. The third child was but 35 cm. long, and weighed but 900 gms. It died very shortly after birth. The placenta was very anæmic. The divisions between the three placentæ were not sharp, but large vascular anastomoses between the placentæ were not present. The placenta of the second child, which survived,

CASE 1: HANDS AND FEET OF TWO-EGG TRIPLETS

Figure 1

X-ray photographs of hands and feet of triplets described as Case 1 in this study. Elsbeth (*A*) and Erika (*B*) are apparently identical and Emma (*C*) is different. A study of the similarities and differences in bone development in the above photographs shows the differences even more strikingly than a study of external physical characteristics.

HEELS AND ELBOW JOINTS OF CASE I TRIPLETS

Figure 2

Profile X-ray photographs of heel and of elbow joints of triplets shown on opposite page (Figure 1). Here again the concordance between the identical pair (*A* and *B*) is striking.

lay in the middle. The placenta of the first child was connected over the chorion by means of large blood vessels to the cotyledons of the placenta of the third. The abnormal anæmia of the one placenta is evidence of deficiency of the placental and foetal circulation. It is a case of environmental intrauterine disturbance of the development of one member of the triplets—a *peristatic* influence. The *X-ray investigation of these triplets* showed: An identical stage of ossification of the ossa ilei, ischii and pubis for all three. The centre for the distal femur epiphysis is identical among the two properly developed foetuses, whereas in the third they are not present. The ossification of tibia, fibula talus, calcaneus, metatarsus was identical in all three. The ossification centre for the middle phalanx for the fifth toe that is usually to be found in the 8-9 month of intrauterine life was absent in all three. The cuboid, which usually shows an ossification centre shortly before or after birth, had not ossified. With regard therefore to their bony development the triplets were concordant with the exception that the lower femur epiphysis was absent in the member which as a result of peristatic influences had remained backward in development.

Five Sets of Triplets

In the following pages we are presenting a study of five sets of triplets: One Class I (uniovular), three Class II (biovular), and one Class III (triovular). The age and sex of these sets is as follows:

Case No. 1, Figures 1-2. Elsbeth, Erika, Emma K—female, Class II triplets, 7 years old.

Case No. 2, Figures 3-4. Oskar, Alfred, Hans Ki—Class II, male triplets, 9½ years old.

Case No. 3, Figures 5-6. Walter, Heinz, Horst Sch.—Class II, male triplets, 11 years old.

Case No. 4, Figures 7-8. Lucie, Anita, Rosalie B—Class III, female triplets, 12 years old.

Case No. 5, Figures 9-10. Pauline, Maria-Theresia, Adelheid A—Class I, female triplets, 4 years old.

Case No. 1, Class II Triplets—7 Years Old

(Figures 1 and 2)

	Elsbeth (A)	*Erika (B)*	*Emma (C)*
Height	118 cm	119 cm	125 cm
Eyes	Identical brown		A different brown
Hair	All three the same		
Ears	Identical		Different

At the birth the father was told that Elsbeth and Erika came in a common amnion, whereas Emma was in a separate one.

The evidence indicates that these are Class II triplets, Elsbeth and Erika being identical. A study of the X-ray photographs brings to light the following concordances and differences:

Hands: The ossification is approximately the same in all. Elsbeth and Erika are slightly more advanced (size and structure of the centres). The form of the centres (capitatum and hamatum) shown by Emma is very different from that of the other two sisters. A similar difference can be seen with regard to the radius epiphyses. The other centres are not sufficiently advanced to allow an opinion. (Fig. 1 left.)

Feet: Elsbeth and Erika are identical and slightly in advance of Emma. The calcaneus apophysis on both sides is less developed in Emma's case than in the case of the other two children. The form of the bones is absolutely concordant in the case of Erika and Elsbeth, quite different in the case of Emma. (c.f. cuneiforme I.) (Fig. 1 right.)

Elbow: Elsbeth and Erika concordant, Emma discordant. (Fig. 2.)

Although Emma is slightly taller than the others, the ossification is a little retarded. The details of ossification shown by Emma are discordant in comparison with Elsbeth and Erika, who are absolutely concordant.

Case No. 2. Male Class II Triplets—9½ Years Old

(Figures 3 and 4)

	Oskar (A)	*Alfred (B)*	*Hans (C)*
Height	139 cm	132 cm	134 cm
Hair	red-brown	fair	fair-brown with a light red tint
Eyes	All identically light blue		
Ears	Oskar's ears are different from those of the others.		

Alfred shows a small hæmangioma the size of a cherry in the mucous membrane of the cheek on the right side. There is no corresponding appearance in the case of the other two.

The similarity investigation shows

that these are probably Class II, Hans and Alfred being uniovular. The osteological similarities and differences, as revealed by the X-rays, are as follows:

Hands (Fig. 3): Oskar is somewhat more developed than the other two. The ulna epiphysis is larger and shows a more advanced bone structure. The cartilages are narrower.

Hans and Alfred show clearly the remains of a pseudœpiphyseal line on the medial side of the second metacarpus. No such line is visible in the case of Oskar. The pseudœpiphyseal lines of the 5th metacarpus are visible in all three, least obvious in the case of Alfred.

Hans and Alfred show an absolute identity in the form of the completed bones. Oskar shows definite differences. (c.f. Capitatum and naviculare.) Since the bones of Hans and Alfred are not yet completely developed, we can make no definite conclusion with regard to the concordance or discordance between these two.

Elbows: The ossification is equally progressed in all three. There is a definite concordance in the form of the radiusepiphyses of Hans and Alfred, whereas Oskar is discordant.

Feet: The ossification is concordant in all three. Hans and Alfred show a definite concordance in the shape of the tarsalia, whereas Oskar is discordant. (c.f. Cuneiforme I.) The ossification of the calcaneus apophysis is more advanced in the case of Oskar. Alfred shows a compacta ring in the left calcaneus, Oskar shows a similar but smaller ring with the same localization. Hans shows a shadow of uncertain nature at the same place.

There is extensive concordance in the skeletal development between Hans and Alfred, whereas Oskar is definitely more advanced. (Ulna-epiphysis, calcaneus-apophysis, carpalia). With regard to the form of the bones Oskar is discordant with regard to the other two, who show a very extensive if not absolute concordance. The slight developmental abnormality in the structure of the calcaneus is present in all three brothers, though not identical.

Case 3. Male Class II Triplets—12 Years Old

(Figures 5 and 6)

	Walter (*A*)	*Heinz* (*B*)	*Horst* (*C*)
Height	139 cm	138.5 cm	139 cm
Hair	Fair, all three very similar		
Eyes	Dark brown	dark brown	light blue
Ears	Both very similar		different
Complexion	Dark	dark	fair (with freckles)

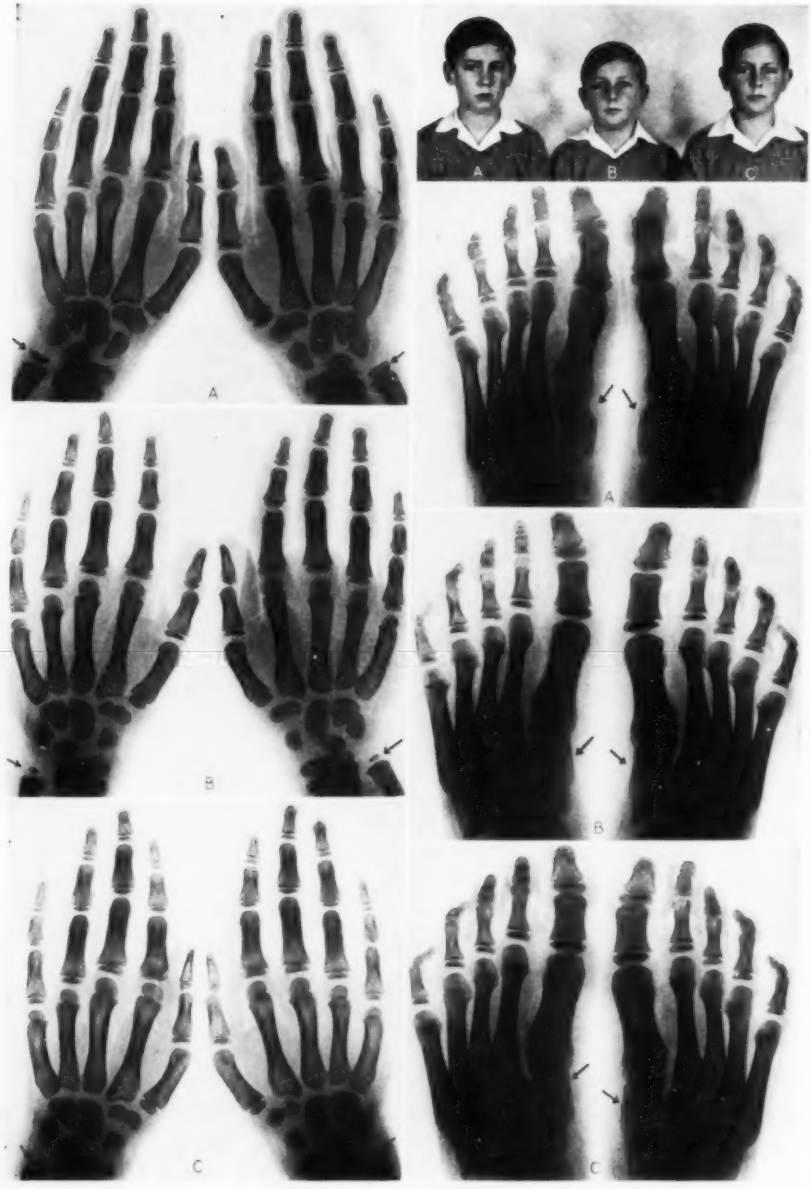
A valid report on the choria was no longer obtainable. The parents say that Horst differs very definitely from the other two children. He is quieter, more sensitive and more sensible. The investigation of similarity shows that this set is Class II, Walter and Heinz being identical in genetic factors, whereas Horst is genetically different.

The X-ray photographs reveal the following significant skeletal similarities and differences:

Hands: All three have reached a similar stage of development. Walter and Heinz show an extensive concordance in the form of the bones, whereas Horst is discordant (c.f. Ulna epiphysis, multangulum majus and navicular). Horst shows an ossification variation: the extra-epiphysis at the posterior margin of the navicular. On the right side, this epiphysis has already partly united with the navicular, whereas the epiphyseal line is easily visible on the left side. Horst shows further pseudœpiphyseal lines in metacarpus II and the remains of epiphyseal lines in metacarpi III-V.

Knees: The development is concordant in all three children. The patella form is concordant in Walter and Heinz, whereas Horst shows a definitely discordant patella.

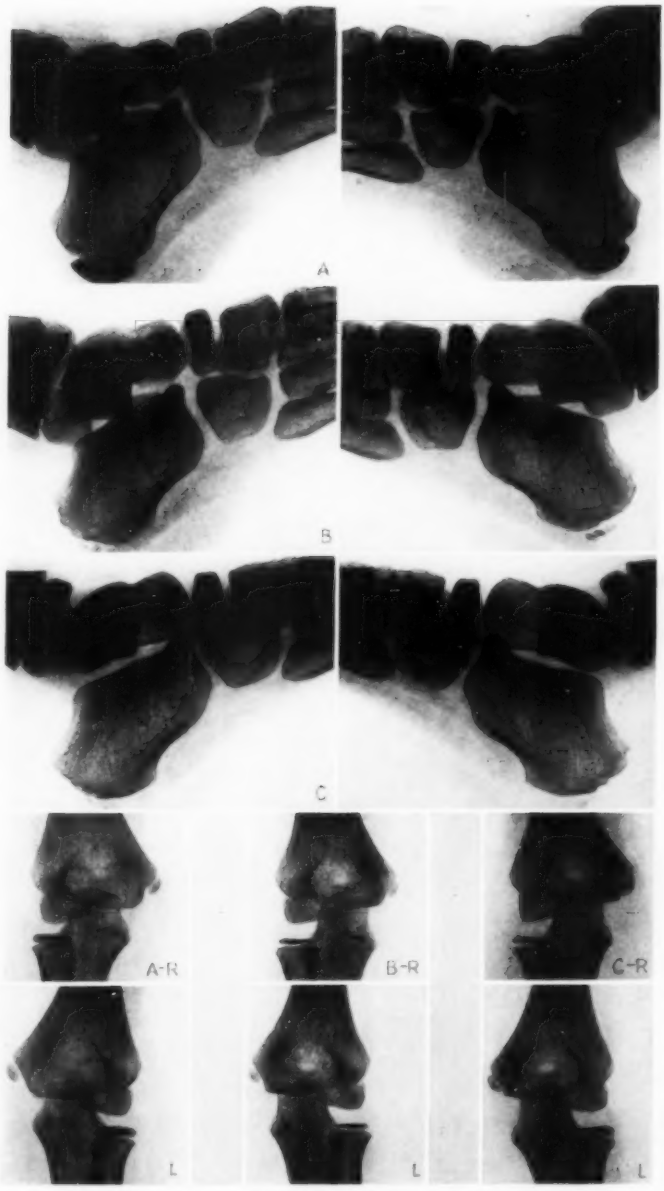
Feet: The ossification is approximately the same in all three. The form of the bones is concordant as regards Walter and Heinz (c.f. cuneiform I and cuboid), whereas Horst is discordant. The sesamoid bones of Walter's great toes have not yet developed, whereas Heinz shows sesamoid bones on both sides. Horst shows the medial sesamoids on both sides. The development of the terminal phalanges is concordant in all three. In the original radiograms a small separate centre of ossification is shown at the edge of cuneiforme I in Walter and Heinz, which is not present in Horst. In the reproductions these centres are scarcely visible. The ossification of the calcaneus apophysis shows no peculiarities. The epiphysis of the proximal phalanx of the big toe on the right side is double in the case of Walter and shows traces of development from two centres in the case of Heinz, whereas in the



CASE 2: ADVANCED BONE DEVELOPMENT IN ONE TRIPLET

Figure 3

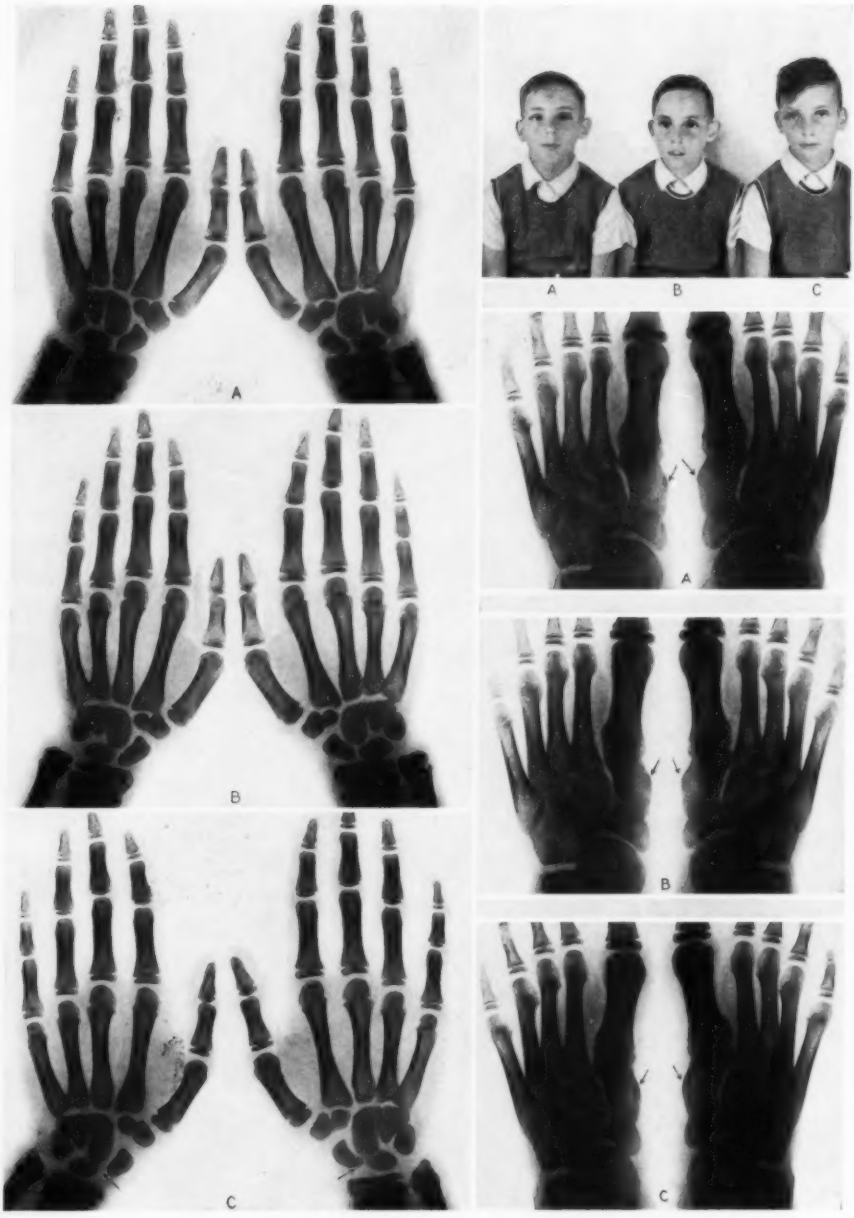
Oskar (*A*), Alfred (*B*), and Hans (*C*), were nine and a half years old when these photos were taken. Here again we have striking similarities between two of the triplets (*B* and *C*), and very considerable differences in the third. Ossification of Oskar's bones (*A*) is definitely more advanced than the other two. In form of bones there are marked differences as well.



CASE 2: HEELS AND ELBOW JOINTS COMPARED

Figure 4

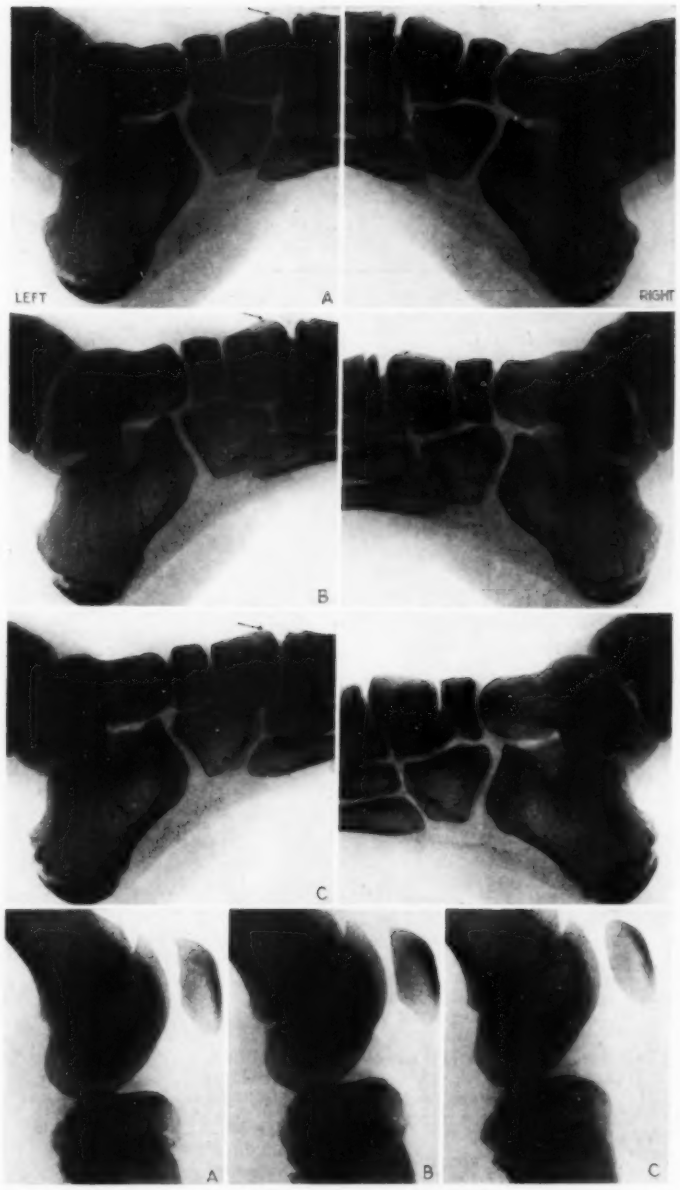
Here again a comparison of the similarities between the identical pair (*B-C*) and the unlike "brother" (*A*) is striking. In all of these photographs of hands and feet the arrangement is the same with the right hand member at the right.



CASE 3—"IDENTICAL TWINS" AND A "BROTHER"

Figure 5

Walter, Heinz, Horst, are eleven year old triplets,—Class II (Biovular). X-ray photographs of their hands and feet show remarkable similarities between Walter (*A*) and Heinz (*B*). Horst (*C*) is the "brother" who developed from a different fertilized egg and who shows characteristic differences in skeletal development.



CASE 3: HEEL (PROFILE) AND KNEE JOINTS

Figure 6

Further similarities in outline is bone shape between the identical triplets, *A* and *B*, can readily be detected. The three left knee joints (lower row) show this contrast very clearly, *C* having a knee cap of very different shape.

case of Horst the epiphysis is built on a different plan and has obviously ossified from one centre.

The uniovular pair, which possess identical chromosome material, show a very definite concordance and a definite discordance with regard to the third partner. The ossification is approximately equally developed in all three. (The slight difference in the ossification of the olecranon cannot, in view of the presence of a difference between left and right, be evaluated.) With regard to the method of ossification, there is a definite difference in the case of the discordant Heinz with regard to the other two (c.f. lunatum and variation in cuneiform I.)

Case 4. Female Class III Triplets—12 Years Old

(Figures 7 and 8)

	Lucie (*A*)	*Anita* (*B*)	*Rosalie* (*C*)
Height	156 cm	148 cm	146 cm
Hair	Fair	Fair	Very fair
Eyes	Moderately brown	Browner	Very brown
Ears		All different	

The mother says she was told that the children all came from different eggs. Data with regard to the choria were no longer obtainable. The development is approximately the same in all three:

Hands: The thumb sesamoids have developed on both sides in the case of Lucie and Rosalie, whereas the development is retarded in Anita. Anita shows a definite pseudœpiphyseal line on the radial side of the metacarpus and Lucie shows but a trace, whereas Rosalie shows none at all. The structures of the completed bones show slight but definite discordances among all three. Anita differs more from Lucie and Rosalie than they do from each other.

Elbow: Definite discordance. Lucie is more developed than Rosalie; Rosalie is more developed than Anita. The same differences are found in the formation of the trochlea, in the case of Lucie it has partially united, in the case of Rosalie clearly formed and with a definite shadow, in the case of Anita the trochlea is only just visible. The formation of the epicondylus radialis shows similar discordances. The order of ossification is the same in all three (radiograms not shown.)

Knee: Discordance in the extent of development of the tuberositas tibiæ-apophysis is found. The formation of the patella is discordant. (Radiograms of the right side only are shown.)

Foot: The ossification is approximately the same in all three. Lucie and Rosalie show two sesamoid bones for the big toe on both sides. The medial sesamoid bone on the left side is split. Anita shows sesamoid bones on the right side; they are not visible on the left.

Lucie has an os tibiale externum on the right side, which the others have not. There is definite discordance in the shape of the completed bones. A special centre for the ossification of metatarsus 5 is visible in all three; in Anita's case it is small. Rosalie shows a small extra sesamoid bone in the region of the talo-navicular joint (c.f. Fig. 8).

There is a slight difference in the time of development of the various ossification centres. Judging by the ossification, the order of development is: Lucie, Rosalie, Anita. The development does not therefore correspond to the height of the child. Growth intensity and ossification do not proceed hand in hand. Sundry small variations in the ossification were found that were discordant. Furthermore there is a definite discordance in the form of the completed bones. There is more similarity between Lucie and Rosalie, than between either of these children and Anita. The two more similar partners with regard to their ossification have also the more similar appearance, although the height difference is greatest.

We must conclude that Lucie and Rosalie have a more similar gene material with regard to that portion which is responsible for ossification and appearance, whereas Anita is in this respect genetically different. On the other hand it is clear that these genes which control ossification do not regulate growth. In this respect Anita and Rosalie are more similar than Lucie.

These conclusions must, of course, be considered to be hypothetical.

Case 5. Female Class I Triplets—12 Years Old
(Figures 9 and 10)

	Pauline (A)	*Maria-Theresia (B)*	*Adelheid (C)*
Height	100.5 cm	99 cm	99 cm
Hair	Fair, straight, identical in all three		
Eyes	Light blue in all three; all three show a strabismus		
Ears	Identical		

A brother of the grandfather on the father's side has three pairs of twins, one pair a boy and a girl, one pair two boys and one pair two girls. It was possible to determine that these were three pairs of biovular twins.

During the birth of these triplets it was noticed that the waters broke before each birth. Maria-Theresia was born in a separate intact chorion. The placenta was of normal size and in one piece.

At the age of 4½ months photographs were made, which showed extraordinary similarity of all three children. Radiograms of the hands made at this time showed an absolutely concordant development (Figure 10). All three showed slight signs of rickets, particularly the ulnae. (I wish to thank Prof. Fanconi for this material and for the opportunity to investigate the triplets.)

Investigation of similarity (Figure 10) shows that we are dealing with definitely Class I Triplets. The osteological development was remarkably alike:

Hands: The development is identical in all three. The order of the ossification, as far as it can be judged from the size of the centres, is concordant. The carpalia show but the slightest differences in form. On the radial side of the capitatum is a slight dissimilarity visible between Adelheid and Pauline, but Maria shows a very similar difference between her own left and right hands. The ossification is not sufficiently developed to regard these slight dissimilarities as discordances. All three children show similar changes in the neighborhood of the radius epiphysis for which the slight rickets was responsible. (Fig. 10.)

Feet: The radiograms show a definite concordance between the three children with regard to the development. It is also visible that the shape of the bones is concordant among all three. The development is somewhat more advanced and permits this more definite conclusion (c.f. cuneiform I and cuboid). (Fig. 9.)

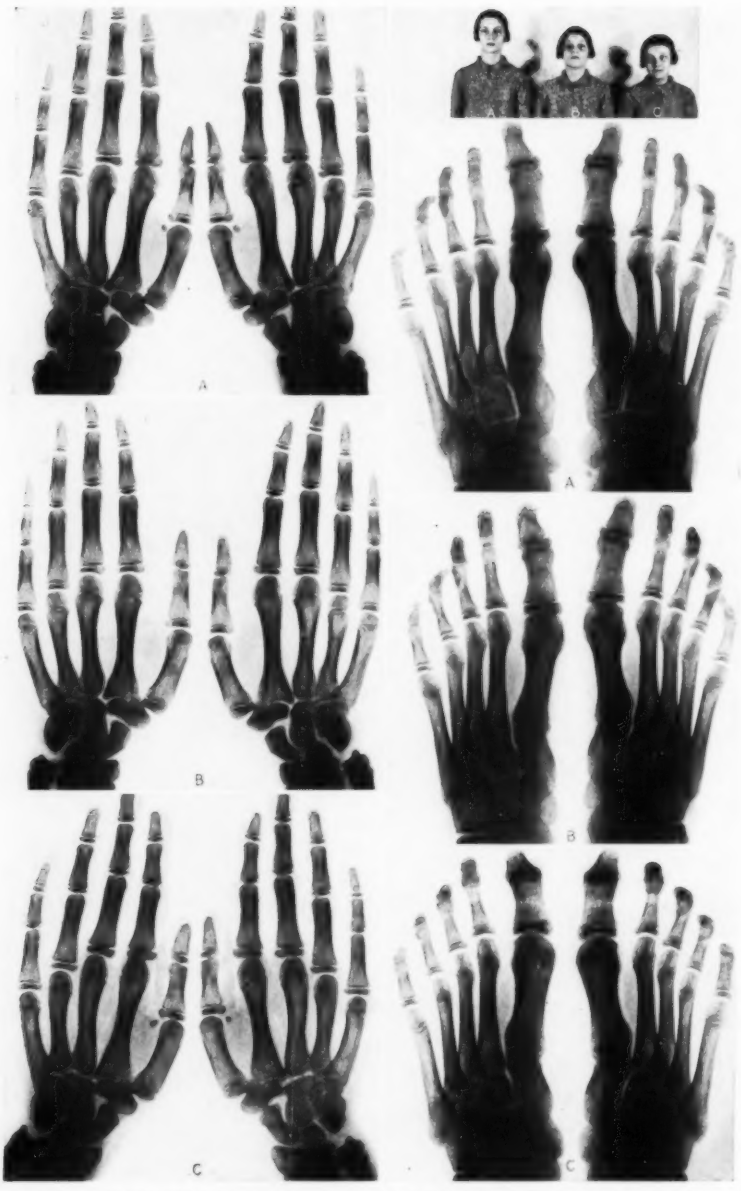
The development of the skeleton is absolutely concordant in this set of triplets. The shape of the individual bones is very nearly concordant. That they belong to Class I and have originated from a single zygote is hardly to be questioned.

Discussion

It is clear that final conclusions cannot be drawn from this small number of cases. Nevertheless a consideration of the results of the investigation of over fifty pairs of uniovular and biovular twins[4] and a combination of these with the results of the investigations of triplets permits certain definite inferences. Conclusions drawn from the triplets are supported by the results of investigation of twins and vice versa. Class II triplets provide an excellent check on the accuracy of the conclusions with regard to twins, for in this case we have "uniovular" and "biovular twins" combined in a single birth to form triplets. These "two pairs of twins" are of the same age and have grown up under the same environment. These cases of biovular triplets permit therefore not only a confirmation of the results of twin investigations, but also make possible conclusions with regard to the influence of heredity in the determination of skeletal development. Such accuracy is not obtainable by comparisons between separate pairs of uniovular and biovular twins, for such pairs of twins are always exposed to different environments and it is impossible to allow precisely for this difference.

Growth

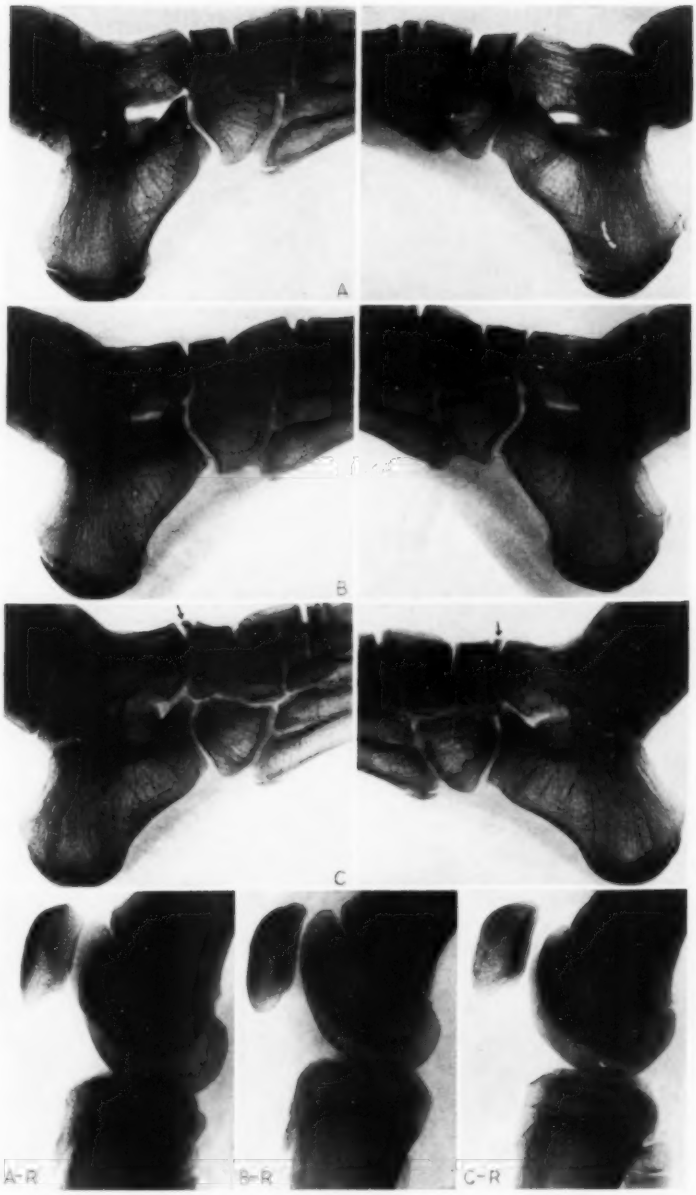
The rate of growth is determined by hereditary factors,—by the gene material. The difference in height between uniovular partners at any given



CASE 4: TRIPLETS PRODUCED FROM THREE SEPARATE ZYGOTES

Figure 7

Three triplet girls—Lucie (*A*), Anita (*B*), and Rosalie (*C*)—were 12 years old when these photographs were made. In skeletal characteristics, as in others, there are no striking concordances between any two of them, though Lucie and Anita resemble each other more closely than either does Rosalie. The differences are not striking, however, and it must therefore be tentatively concluded that we are dealing here with Class III triplets, produced from three separate fertilized eggs.



CASE 4: DISCORDANT BONE DEVELOPMENT IN TRIPLETS

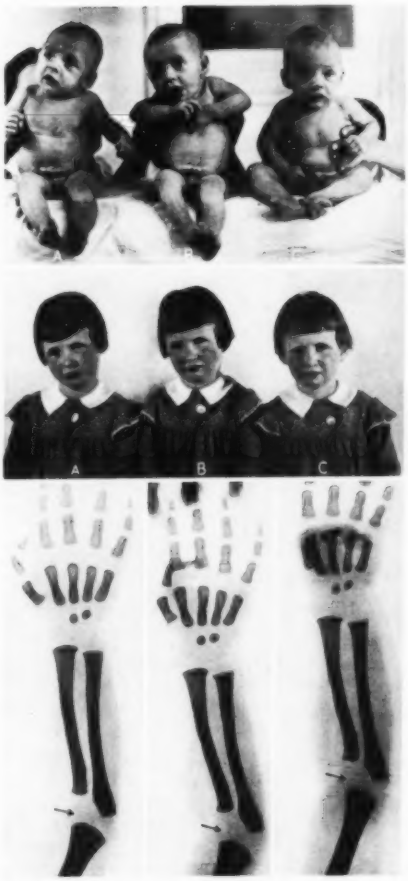
Figure 8

Heels and knee joints of the three girls all show distinct characteristics indicating further that they owe their origin to the development of three separate zygotes. This case should be carefully compared with Case 5, in which all three triplets show remarkable resemblance. Studies of these cases are important because they show the range of genetic variation which may occur in spite of a similar interuterine and post natal environment in physical development.

CASE 5: THREE WITH AN IDENTICAL GENETIC CONSTITUTION

Figure 9

Pauline (*A*), Maria Theresia (*B*), and Adelheid (*C*), are strikingly alike in external characteristics and in bone development at an age of four years, when these photographs were made. There appears to be little question that they developed from a single zygote, which separated into three growth centers early in embryological history. See also Figure 10.



TRIPLETS AT FOUR AND ONE HALF MONTHS AND FOUR YEARS OF AGE

Figure 10

Photographs of Case 5 triplets at 4½ months and 4 years, and (below) an X-ray photograph of the hands made at the time the first picture was made (4½ months). This shows that the bones at that age were exactly similar in development. There are slight signs of rickets, equally extensive in each of the triplets, to be seen in the development, particularly of the ulnae.

age is always less than the difference between multiovular partners of the same age who have grown up in the same environment. The average difference in height between uniovular twins was found to be 1.2 cm. in the material that I investigated,[4] whereas the biovular twins showed an average difference of 2.7 cm. Furthermore, there is in Class II cases a slighter height difference between the "uniovular partners" than there is between these and the third partner. Thus in Case 1 the difference between the "uniovular partners" is 1 cm., whereas the third partner shows a difference of 6 (7) cm. A similar situation is found with regard to the children in Case 2, where the "uniovular partners" are within 2 cm. of each other, whereas the third shows a 5 (7) cm difference. On the other hand in Case 3, also belonging to Class II, there is no difference in height of any of the partners, whereas of the Class III, Case 4, two of the partners show similarity with regard to height, differing from the third. The uniovular, Class I set (Case 5), shows, as would be expected, concordance among all three partners.

Mode and Rate of Ossification

The development of the ossification centres serves as an indicator for the *rate* of bone formation in the skeleton. There is a general stage of bone development which corresponds to the age of the child, which is to be regarded as "normal" for a certain age and sex. This condition is an expression of a normal rate of ossification. This rate is faster in girls than in boys. Girls therefore show a more advanced stage of ossification than boys of the same age.

This normal rate of ossification is remarkably constant in healthy children who have suffered no illness. The precision and accuracy of this ossification pattern is remarkable, even when the children show considerable differences in size. A comparison of the skeletons of the triplets shows this point very clearly, as it was also shown in the investigation of twins.

In addition to this normal rate of ossification, which leads to a normal

degree of bone development for a certain age, there are details of the *type* of ossification of single portions of the skeleton, that may show very clearly individual differences. But it is clear that these differences also are determined by the gene material and are not noticeably dependent on environment. The Class II sets provide an instructive example for this thesis. Thus the "uniovular partners" in cases 1 and 2 show a complete concordance in the ossification of the calcaneus apophysis, whereas the third partner is very definitely discordant. The identity between the two cases is so striking that it is hardly possible to regard it as due to chance. In case 1 the "uniovular partners" show complete concordance with regard to the development of the carpalia, whereas the third partner is discordant. This discordance is slight, but must, in view of the complete concordance of the other two, be regarded as an expression of the influence of genotype factors. Similar conclusion can be made with regard to the ossification of the ulnar epiphysis in the triplets of Case 1. *In all these cases there is a definite concordance between the partners that possess identical genetic factors, and a discordance with regard to the third (genetically dissimilar) partner.*

The Relation of the Rate of Ossification to General Growth

I have shown that the differences in development in these triplet sets prove that the rate of general growth and that the rate of ossification are determined by genetic factors. Growth and ossification seem to be regulated independently of each other. But the smaller partner, with a slighter tendency to general growth, usually shows a retardation of the ossification (c.f. Case 3). On the other hand, partners that are equally tall show definite differences in the ossification. These differences are much more marked between partners that have not sprung from the same egg. This fact was clearly demonstrated in the investigation of twins and in Case 1, reported above, it again appears. The "uniovular partner" who is easily the tallest of the three, is not nearly so advanced with regard to the ossification of the whole skeleton. A similar conclusion may be drawn from the triovular set in Case 4. Although one of the children is intermediate in height as compared with her "sisters," with regard to their height she is definitely retarded in extent of ossification as compared with them.

These observations, which are completed and supported by the results of the investigation of twins, show that growth and ossification are regulated independently. The fact that the "ossification pattern" follows more definite and constant laws, that is, laws that are valid for the whole species, whereas growth is a very individual matter, supports this view.

Qualitative Variations in Ossification

Variations in ossification are probably subject to genetic factors. Of this the Class II Case 3 provides a good example, where a small ossification variation of the carpalia (separate centre of ossification for the os naviculare) is only to be found in the partner with separate and distinct genotypic factors. The others "uniovular" have no such variation (c.f. Figure 5). In the same case the uniovular partners, with identical genotypic factors, show a small variation of the ossification of cuneiform I. The variation is to be found on both sides. The third child, with a different genetic constitution, shows no such variation (c.f. Figs. 5-6).

During the twin investigation I noticed the whole series of ossification variations. These variations were concordant in the uniovular twins and discordant in the biovular twins. Of practical importance in this connection is an aberrant ossification of cuneiform I, which is related to the juvenile osteochondropathics (Morbus Köhler, Morbus Schlatter etc.).

It is impossible to be certain whether the pseudoepiphyses belong to this

group. As a result of the investigation of twins, I think these pseudoepiphyses are to be regarded as physiological. The time of their appearance is variable and it is a matter of chance to demonstrate their existence. The variations with regard to these pseudoepiphyses fall apparently into the category of variations in the *rate of growth* and not into the category of variations in the *mode of growth*. The question must be regarded provisionally as undecided. In any case the pseudoepiphyses cannot be regarded as pathological. It is clear that genetic factors determine the appearance of these pseudoepiphyses. In Case 3 (Class II) the "unlike partner" shows a pseudoepiphysis to metacarpus II and a trace in metacarpalia III-V. The other two, "uniovular," and consequently genetically alike, show no pseudoepiphyses. In Case 1 (Class II) the two homologous partners are less developed with regard to their ossification and show a pseudoepiphyseal line in metacarpus II, whereas the third more advanced member of the trio does not show this line. On the other hand all members of the trio show a pseudoepiphyseal line in metacarpus V. The absence of a pseudoepiphyseal line in metacarpus II in this child can be regarded as being due to the more complete development of the ossification. It is not necessary to consider it as a qualitative variation in the ossification. We are not, therefore, in a position to conclude with certainty that the rate of uniting of the pseudoepiphyses is the only genetically controlled characteristic.

The Determination of the Shape of the Completed Individual Bones

The extent to which the shape of the bones is determined by genetic factors is clear from a consideration of the concordance in shape of the bones of two homologous members of a trio and the discordance with regard to the third. The pairs possessing the same chromosome material show concordances in this respect that extend to the smallest details (c.f. cuneiform I in Cases 1 and 2, the radius epiphyses in Case 1, the patellae in Case 3).

Summary

1. The results of the radiological investigation of the skeletons of five sets of triplets (aged 4½ months to 12 years) are reported. The material consists of three trios of biovular triplets, one trio of triovular triplets, and one trio of uniovular triplets.

2. The results of this investigation confirm the results of a similar investigation made by the author of fifty pairs of twins. In this investigation the biovular triplets were particularly instructive.

3. General growth and the rate of ossification are controlled by genetic factors. They are controlled independently of each other.

4. The qualitative variations in the ossification and the shape of the completed individual bones, including the finest details, are also determined by genetic factors.

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THE SKOPTZY SKELETON

EVER since Tandler and Gross in 1909 published their classical account of the skeleton of a eunuch, it has been known that early castration has profound effects on growth of the male body. The most extensive "experimental" material of this kind is provided by the Skoptzy, a Russian and Roumanian sect in which all male members are castrated. Pittard* presents the results of an anthropological study of over one hundred Skoptzy. A racially similar group of normal adult males served for comparison. The Skoptzy were nearly evenly divided into two groups, the first comprising those individuals in which castration had been performed previous to sexual maturity, while in the second group are those men which were castrated after sexual maturity had been attained. Due to the secrecy surrounding the sect and all its activities, it was, unfortunately, impossible to obtain exact data concerning the time of castration, but there is unquestionably a sharp demarkation between these two groups. Those who had been castrated before maturity show the typical features of eunuchs, while those castrated later can scarcely be distinguished from normal individuals. Pittard's work provides abundant evidence for the well known effects of early castration: great body height, great length of the extremities (relative to trunk), lack of facial and axillary hairs, unbroken voice.

Pittard's most important contribution consists perhaps in extensive data concerning the relative length of the extremities. It appears that the face of Skoptzy (height and width) is larger than in normal individuals of similar height. There are many other interesting observations. In some instances, however, the author's conclusions are open to doubt. It is found, for instance, that the skull of the Skoptzy is smaller in all its dimensions, and, on the basis of comparisons with normal men of similar height the smallness of the skull is interpreted as an effect of castration. The validity of this, and of similar conclusions with regard to other traits, seems doubtful since these Skoptzy, if it were not for the excessive length of their long bones, would represent a group of much lower body height than the controls with which they were compared. The introductory chapters of the book contain a general (rather sketchy) survey of the effects of castration on growth and an interesting history of the Skoptzy.

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*PITTARD, E., *La castration chez l'homme et les modifications morphologiques qu'elle entraine. Recherches sur les adeptes d'une secte d'eunuques mystiques, les Skoptzy.* Paris, Masson et Cie., 1934. 329 p., 70 figures, 143 tables. 60 francs.

THE PRODUCTION OF BARLEY SEED THROUGH POST-HARVEST POLLINATION

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BARLEY PRODUCED BY POLLINATION AFTER HARVEST
Figure 11

The four hybrid spikes shown here (531 × 139, etc.) were grown from seeds produced from spikes pollinated after harvest (see Figure 12). It would seem that the plant breeder must add to the tools of his trade a vase for cut flowers in which to raise seeds when field conditions are unfavorable!

IT HAS been found that immature barley kernels make a considerable growth both in embryo and in endosperm after harvest.* This growth is much greater where the culm bearing the spike is kept moist and still greater if the cut end of the culm is left standing in water. Since normal nutrition is interrupted and fungi may invade the cut end, the life of such a culm is shorter than that of an unharvested one.

Culms harvested and placed in distilled water when the spikes were beginning to flower lived for a considerable time and produced kernels. In these, necrosis proceeded as in normal culms, that is, from lowest leaf tip toward the node and in like manner the upper leaves in order. The nodes and kernels re-

* HARLAN, H. V., and M. N. POPE. Development in immature barley kernels removed from the plant. *Jour. Agr. Research* 32 (7): 669-678, illus. 1926.

BARLEY SPIKES FROM POST-HARVEST POLLINATION

Figure 12

Four spikes of Hannchen barley emasculated and pollinated after the culms had been removed from the plants at about the time the flowers were mature.

mained green for some time after the death of the leaves.

On April 4, 1934, four spikes of the 2-rowed Hannchen barley, C.I.* No. 531, with unripe pollen, were harvested, placed in a flask of distilled water, and emasculated. Two days later, when most of the stigmas were receptive, these spikes were dusted with pollen from spikes with extruding anthers. Two of these male spikes were 6-rowed awned types (C.I. 5981 and 5982) and two were 6-rowed hooded (C.I. 5979 and "Hooded 139").

* C.I. refers to accession number of the Division of Cereal Crops and Diseases.

Fertilization of the flowers was evidenced in a few days by growth of kernels in the four post-harvest pollinated culms. On several occasions about one inch was cut off the immersed ends of the culms to prevent clogging of vessels with mycelia.

On April 25, 21 days after the culms were harvested, they were photographed (Figure 12). At this time nodes and kernels and more than half of the boot leaf sheath, together with portions of the lower leaves, were still green. The lemmas were beginning to lose color and on one spike the green of the tip kernels was fading. On April 27 the kernels were losing color rapidly though the flanks were still light green and the crease area, deep green. By May 2 the culms were practically dry and the green was rapidly fading from the nodes. The next day, as the kernels were drying down rapidly, the spikes were cut off and stored. Average air dry weight of these seeds was about 19 mg. as compared with 53 mg. for well-matured Hannchen kernels grown under similar conditions.

In the fall of 1934 seeds from each of the four spikes were planted in pots in the greenhouse. These plants produced spikes which showed their hybrid character (Figure 11), leaving no doubt that viable seed can be produced by pollinating flowers of barley plants harvested before the anthers have dehisced.

Possible applications of this phenomenon in the course of practical plant breeding work are apparent.

ORIGIN OF THE BASQUE PONY

AN amazing labor of scientific erudition is a recently published treatise on the Vasco Pony.* The vast scope and the painstaking details of this article may be realized faintly by a brief enumeration of some of the subject captions, viz: "Agriculture of the Vasco Country," with sub-headings of "The Land," "Agriculture," "Observations about the Woods and Fields," "Table of Climatic Conditions," "Table of the Distribution of Rural Population," numerous tables giving density of the "Rural Population," number of houses, single and double, and the acreage of various provinces. He then describes the "Conditions under which the Vasco Pony Lives." Then follows a "Necessary Explanation" (which as the article develops seems to be an unnecessary explanation) to show how complicated is the attempt to determine the ethnological origin of the Vasco Pony, after which the author goes into the "Paleontology"—that of the "Old World" and that of the "New World," —amplified with geologic tables and a description of the nature of the fossils found. He then describes the primitive type of the horse, quoting the theories of well known scientists—English, American, German and various other nationalities.

That the reader may more easily visualize the trend of the argument numerous maps are interspersed showing geological and ethnological conditions at various times since the Tertiary Period. Then follow cuts of some of the well known cave drawings of horses and of artifacts showing horses heads carved on sword hilts; photographs of the Przewalski horse and a drawing of the Tarpan.

To state that like data with ever increasing detail, especially on the subjects of the head and the dentition, are sustained, in all the various ramifications of the argument, throughout 148 pages, is enough to indicate the enormous labor accomplished in this research.

* FERRERAS, G., *El Caballo Vasco—Su Origen y Relaciones con el Caballo Oriental y Occidental* (The Vasco Horse, His Origin and Relations with the Oriental and Occidental Horse.) Ganaderia Vasco, Vol. I Zootecnia. Bilboa, 1935.

While this brief notice is no attempt at an adequate review of the Vasco Pony article it is only fair to the reader to try to give him an idea of its objectives. Among other points the author endeavors to show from what type of primitive horse the Basque pony descends; its identity with certain of the prehistoric drawings of horses found in the caves of France and Spain; its relation to various historic breeds including the Arabian and the Barb; and the country where it was first domesticated.

The author's general conclusions given at the end of the article are here freely translated:

1st. The Vasco pony possesses a decided phenotype, a uniformity that proves the scanty intervention of alien races.

2nd. The analysis of the osteologic characteristics demonstrates the fixed genotype of the Vasco horse group, to the very end of such evidence.

3rd. The existence of the Vasco pony is established in this region (Spanish Basque provinces) and in that of the French Basque country as early as the paleolithic era, drawings of which were unearthed in Santimamine and in the south of France showing clearly fragments which constitute incontrovertible evidence.

4th. The origin of the Vasco pony took root in those villages where it had been introduced, which conforms to the thesis of Adamatz and also to that of Kronacher showing that it belonged to the Oriental group and in no way should be considered as an indigenous species (span. autoctono). Its domestication does not seem to have begun in the Basque country. This same conclusion has been reached about the Pyreannean and the Cantabridgian horses, of which the more ancient type, if it were possible to recognize it, would be the brother of the Vasco.

5th. If between the Vasco horse and the Sorian horse there should exist any relationship, the study of the evolution of the Tarpan, to which Staffa attributes the Sorian horse, is essential.

6th. The Vasco pony pertains to a small type, strong, robust, entirely different from the Iberian-Berber horse of Adametz, the North African horse of Ridgeway and later of the Spanish Libian; the domestication of this latter form took place in Libya; one derivation from this group is the Arab of relatively recent origin.

7th. The present form of the Vasco horse is of little usefulness; it does not merit a continuance of the type; and if it is cross bred with adequate breeds, it will bring out its few desirable qualities, thus increasing size, capacity, and strength, needed qualities, it alters to that extent the existing type.

8th. The most necessary change which should be brought about in the Vasco horse, and in general this horse group of the North Spanish mountains, is the crossing with types of semi-draft breeds which we meet with in the artillery-agricultural horse.

9th. This cross breeding should be effected in general upon related breeds without bringing about the elimination of the indigenous type following the formation and selection of pure strains thus seeking to obtain a uniform type by the end of the third generation.

To show just how successful the author has been in his arguments and how valuable are his conclusions would require a more prolonged and intensive study of his long and intricate article than this brief notice permits.

THORNTON CHARD

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Exercises in Genetics

THIS manual* by the director of the Institute for Human Heredity and Eugenics at the University of Griefswald provides detailed material for twenty-five assignments in an elementary genetics course. These range from elementary statistical methods to breeding experiments with Drosophila that demonstrate crossing-over and multiple allelomorphs. Any instructor should find the book suggestive.

PAUL POPENOE

*JUST, GUENTHER. *Praktische Uebungen zur Vererbungslehre.* Second edition. Pages, 137, 55 illustrations. Price, RM 6. Julius Springer, Berlin, 1935.

POLYDACTYLY IN SWINE

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AN EXTRA TOE ON EACH FRONT FOOT
Figure 13

A rare anomaly is here shown in an extra toe located almost centrally between the dew claws on the front feet. This appeared irregularly when certain closely related individuals were mated. That a genetic basis exists for the anomaly is certain, but the mode of inheritance is not clear from the data at hand.

POLYDACTYLY in swine is extremely rare. Thirteen instances of this unusual anomaly have been observed among Duroc Jerseys in the California Experiment Station herd. The author has seen one other Duroc Jersey, Maxine Clipper, Junior Champion at the National Swine Show in 1931, with an extra toe on the left front foot. Only one reference to this condition among hogs has been found in the literature, a case reported by Curson* in South Africa. Two front feet of a pig with an extra digit on each were sent to him by one of the government veterinary officers. The extra digits as described by him were larger than those seen by us. He did not mention the breed of the pig nor did he make any attempt to trace the lineage or to explain its mode of inheritance.

In the California Experiment Station, herd boar 10 (Figure 14) was farrowed in the fall of 1927. He was sired by boar 1 and out of sow 2. Because his sire and dam were outstanding individuals, he was saved and used in the California Station herd. He had an extra digit on his left front foot. He was mated to sixteen sows all of them closely related. The offspring of sow 11 were the only ones to exhibit extra toes. This sow

*CURSON, H. H., 1931. *Anatomical Studies*, No. 19, Polydactyly in a Springbok and a pig. Seventeenth Report of the Director of Veterinary Services and Animal Industry, Onderstepoort, Pretoria, 853.

farrowed nine pigs, four boars and five gilts. Three of the boar pigs had extra digits (litter A). Boar 19 and litter sisters 12 and 13 were saved. They were mated and produced litters C and D (Figure 14). Sows 20 (Litter C) and 27 (Litter D) produced two litters each (Litters E, F, G, and H) by boar 19, their own sire. In spite of the close inbreeding (litter mate and daughter sire matings) no offspring with extra digits appeared in these litters.

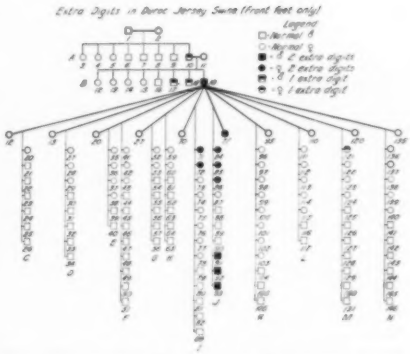
Boar 19 was also mated to sow 70, his own daughter, though not out of sows 12 or 13. Thirteen pigs were produced from this union, two of the gilts having extra toes on both front feet. Sow 71 from this litter was bred to boar 19, her sire. Both had extra digits on each front foot. Ten pigs were farrowed (Litter J) and of this number, three male and three female pigs had extra toes on both front feet.

Sows 95, 110, 120 and 135 were bred to boar 19. Except for gilt 121 out of sow 120 none of the offspring exhibited extra digits. Gilt 121 had one small extra toe on her left front foot. The dam of sow 120 was sired by boar 10. Only thirteen individuals in a population of 125 offspring (Figure 14) had extra digits, and of this number 7 were males and 6 were females. Four boars and five sows had extra toes on both front feet while three boars and one sow had them on only one, and without exception it was on the left foot.

Figure 13 is a photograph of the front feet of boar 19 when he was about five months of age. The position, size, and shape of the extra digits located above and midway laterally between the two dew claws is typical of this anomaly as it appears among Duroc Jerseys in the California Station herd except that certain individuals have it on one foot only.

Record of Ancestry

The pedigrees of boar 19, sow 70, and of Maxine Clipper are presented



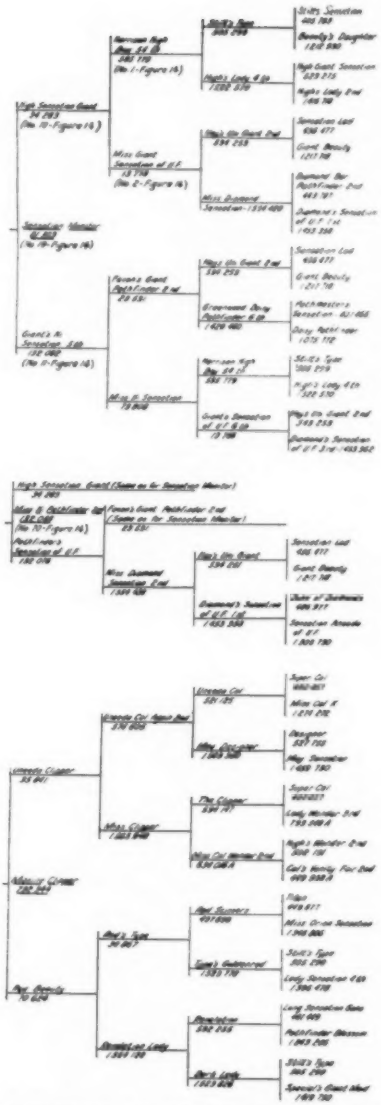
RELATIONSHIP OF FOUR-TOED PIGS

Figure 14

A graphic summary chart of the representative matings, the litters farrowed, and the condition of the progeny with respect to normal and extra toed individuals. Letters designate litters; numbers represent individuals. On the opposite page are shown critical pedigrees for important individuals in this chart.

(Figure 15) to show their relationship and, if possible, to correlate the appearance of five toes with some family of Duroc Jerseys.

The ancestry of boar 19 and sow 70 are similar. Harrison High Boy 54th (Boar 1—Figure 14), appears as the grand sire on the sire's side and as the sire of the grand dam on the lower half of the pedigree of Sensation Monitor (Boar 19—Figure 14). Boar 1 (Figure 14) appears only as the grandsire on the sire's side of the pedigree of Miss Hi Pathfinder 2nd (Sow 70—Figure 14). When these two individuals (Boar 19 and sow 70) were mated, two gilts with extra digits resulted. However, when Sensation Monitor (Boar 19), was bred to his litter sisters, and when two of the offspring of these matings were bred back to him, none of the offspring exhibited extra toes. If the factor for extra toes was a simple recessive it seems certain that more offspring would have exhibited extra toes when boar 19 was mated to his litter sisters or his own daughters, than when he was mated to sow 70; however, this was not the case. Maxine Clip-



ANCESTRY OF POLYDACTYL PIGS

Figure 15

Pedigrees of boar 19, sow 70, and Maxine Clipper. The pedigree of sow 70 is the same as that of boar 19, except on the dam's side of the dam.

per, bred and raised in the Middle West, had one extra toe on her left front foot. She does not appear to be closely related to the pigs showing the anomaly in our herd, although Stilts Type, the sire of boar 1 (Figure 14) appears twice in the fourth generation on the dam's side of the pedigree of Maxine Clipper (Figure 15). If other individuals with extra digits, having similar pedigrees to those presented herein, could be located and reported, it would aid in attempting to locate what family or individual is responsible for it.

No authentic information can be secured that polydactyly had ever been observed in any of the herds of swine maintained at the California Station before Boar 1 (Figure 14) was used as a sire. In neither boar 1 nor sow 2, were extra digits expressed phenotypically, however, boar 10 (Litter A), from this union, had an extra toe on his left front foot, a phenotypic expression of polydactyly. Sow 11 was a normal, four-toed individual but when mated to boar 10, a litter was produced (Litter B) in which three boar pigs had extra digits. Boar 19 had extra toes on both front feet and boars 17 and 18, on the left foot only. None of the offspring in litters C, D, E, F, G or H had extra digits even though they and their mothers were all sired by boar 19. The dams of these litters did not manifest this anomaly.

Sow 70 bred like the pigs in litter B, except on the dam's side of her dam (Figure 15), when mated to boar 19, produced two gilts out of a litter of thirteen that had extra digits on both front feet. (Litter I). This was the first time that females exhibited extra toes in this herd. Gilt 71 out of this litter, was bred to her sire (Boar 19), both having extra toes on each front foot. Phenotypically six of the offspring (three boars and three sows) from this mating were like their parents (Litter J). The others were normal, four-toed pigs. Up to this time we believed the factor for polydactyly in swine was probably recessive, since it was expressed phenotypically so seldom. If, however, the factor for

polydactyly was a simple recessive, all the pigs in this litter (Litter J) should have had extra digits. If boar 19 and sow 71 were simple recessives, the result of this mating can only be explained on the premise that some disturbing agency did not allow the character to be expressed in the normal four-toed offspring in litter J.

Sows 95, 110, 120 and 135, the latter being a litter mate of sow 70, were very closely related (all of the Duroc Jerseys in this herd having descended from two related sows). They were all bred to boar 19 (Figure 14). The offspring from these matings were all normal, four-toed pigs except gilt 121 out of sow 120. She had an extra digit on the left, front foot only.

While there is a population of 125 offspring in this study, the expression of extra digits has been so irregular it is not possible to postulate a definite analysis of the mode of inheritance of polydactyly in swine. Whether the appearance of extra digits in swine is due to a single factor, complementary factors, multiple factors, or on the basis of an inhibitor which prohibits the factor for polydactyly to be expressed is yet to be determined.

Unfortunately, boar 19 is dead and boars 91, 92 and 93 (Litter J) were weak at birth and died soon thereafter. Boars 87 and 88 are still in the herd; likewise, sows 71, 84, 87, 95 and 120 (Figure 14). They will be used in an effort to obtain more data, which, added to that now available, it is hoped will make clear the mode of inheritance of polydactyly in swine.

Summary

Thirteen cases of polydactyly of the forefeet in Duroc Jersey Swine have been observed in a population of 125 offspring. The expression of extra digits was so irregular that no attempt has been made to analyze the mode of inheritance of this anomaly. The anomaly was found about equally divided among males and females.

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THE THIRD STEP TO PROSPERITY

What can be done to bring about better conditions, and provide legitimate work for all? The answer seems very simple to a statistician:

The first and immediate step should be to increase the production and reduce the price of homes, furniture and the thousands of other things which America wants more of today. Only as there is more produced is there more to divide.

The second step should be to move people from the few industries where there is over-production—as in the case of coal, textiles and certain farm products—and subsidize new industries to employ these people. Any other plan simply increases unemployment in these present over-manned industries.

The third step should be to reduce the birth rate among the chronic unemployed and increase it among those able to support themselves. The fewer there are in the submerged, unemployed and low-wage groups, the greater the income will be for those in said groups.

In the following equation, G = goods produced, N = number of families in the submerged group, and I = the income in the terms of food, clothing and shelter of each family in said group. The equation is:

$$\frac{G}{N} = I.$$

It is "I" which should be increased. This can be done ONLY by increasing "G" or by decreasing "N." Moreover, by doing both is the simplest and surest way of reaching the goal. Is it surprising that a statistician is impatient with slap-dash and ill-advised legislation? Moreover, I say this only with the good of the greatest number in mind, and not in the interests of any one group—rich or poor. *Of course, in the end, only as love for others increases will our troubles decrease!*

ROGER W. BABSON.

GENE AND PARASITE PATHOLOGY

Reviewing Two Recent Summaries of the Role of Parasites and Genes As Causes of Disease

THEOBALD SMITH ON DISEASE

THE recent death of Theobold Smith has called forth numerous appreciations of his work, and in another place the reviewer has summarized his research in the field of animal parasitology. In this it was shown that Smith did some remarkable things in the field of parasitology in spite of the fact that he was not a parasitologist in the sense in which the word is ordinarily used. In his last book, *Parasitism and Disease** he still appears as an unconventional sort of parasitologist, and his untrammeled outlook gives the book a most unusual character.

Smith's point of view is indicated in his introduction as follows: "It had long been my desire to bring together all alien invaders and parasites of the animal body and deal with them and the disturbances they produce under some unifying principle." This he has done, taking as his unifying central thought the concept of parasitism. As a result he has dealt with animal parasites, bacteria and viruses from an angle that the bacteriologist and pathologist seldom view them. The inclusion of bacteria and viruses in the same grouping as the more "conventional" animal parasites has presented a subject matter with which the parasitologist is not too familiar and gives much food for thought. The book should be read slowly and questioningly, for the problems it raises are far in excess of the solutions it affords. This is not to deny the merit and importance of the solutions which Smith presents. They are always interesting, and if they sometimes are not convincing it is obviously because the author is still playing the rôle of pioneer and attempting new and unusual things. For evaluating some of his concepts we still have inadequate data. There is no doubt that he has produced a very worthwhile book by putting into juxtaposition a vast body of data not previously assembled under the general theme of parasitism. If its greatest value proves to be in suggesting many lines of new research, this is no small contribution.

The book shows the advantage of Smith's wide background. Primarily trained as a physician, his early work in a veterinary organization, the Federal Bureau of Animal Industry, and his later work in the Rockefeller Institute for Medical Research enable him to draw his facts from human and veterinary medicine alike, and in addition he ranges the field of zoology rather widely. In spite of his pioneer research on animal parasites, Smith was more at home in bacteriology than in parasitology, and his terminology in the field of animal parasites is sometimes impressionistic rather than accurate. Thus he refers to the sclerostomes as "hookworms," although the sclerostomes are not hookworms. The horse and its relatives are parasitized by sclerostomes and not by hookworms, whereas man, dog, swine, sheep and cattle are parasitized by hookworms and not by sclerostomes. His discussion of the life history of the hookworm is lacking in accuracy.

Occasionally Smith subscribes to the concept, more or less popular among certain parasitologists, that normally parasitism is relatively harmless to the host. This is not sustained by the reviewer's experience in the field of parasitology extending over thirty years.

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*SMITH, THEOBALD. *Parasitism and Disease*. Pages, 196. Princeton University Press; Oxford University Press, 1934.

Parasites range in their effects on the host organism from being quite promptly lethal to being apparently harmless (with emphasis on *apparently*). Smith clearly concurs in the idea of harmful parasitism in some parts of the book. He divides the habits of obtaining food into the predatory and the parasitic, ignoring what the zoologists have called the scavenger and the worker types of animals, and then goes further and seems to identify the predatory habit with the parasitic habit. The results are interesting, but somewhat confusing, and one feels that in a treatise on parasitism it would have clarified matters to some extent had "parasitism" or "parasite" been defined; the reviewer finds these terms used in the book in ways hardly justified by dictionary definitions. Similarly, Smith's statement that parasitism is "normal," and not abnormal, calls for a definition of normal. In spite of the reviewer's disagreement with some of Smith's statements, most of these points are presented in a manner that is very stimulating to thought.

In his consideration of life cycles of parasites, Smith states that the host's skin is the portal of entry for most of them. Whether this is true for bacteria is a point which bacteriologists would have to decide. It is not true of animal parasites, of which the majority use the mouth as the portal of entry. In this chapter his table of bacteria and fungi is actually a table of these organisms and of pathogenic diseases—staphylococci and streptococci being listed as coordinate with glanders and leprosy. The data on animal parasites in this chapter are quite frequently inaccurate, and are evidence of the fact that Smith accomplished unusual things in research in parasitology without acquiring a parasitologist's background of fact. In spite of errors, this chapter contains some basic reasoning which deserves careful consideration.

In his third chapter, on aberrant parasitism, the reviewer is impressed by the fact that the man who first recognized *Piroplasma bigeminum* and gave it its specific name refers to it as the American piroplasm, although it had been known for a year or two before his death that there were two piroplasms in cattle in the United States, *P. bigeminum* and *P. argentina*, and that in his original work Smith had seen and figured both of them without recognizing that there were two species. It is also of interest to consider Smith's statement that aberrant parasitism is of less importance to man than to closely related species of animals, and that our domesticated animals are zoologically so distant that few parasites have been exchanged with us. Actually, man has the longest list of known animal parasites, and he has acquired some of those from domesticated sheep or cattle, carabao, swine, dogs and cats, as well as from monkeys, rats and various other wild animals. Nevertheless, Smith has outlined some fascinating possibilities in connection with the transfer of parasites and with the changes in parasites that might be brought about by certain experimental procedures. The dangers Smith cites as consequences of aberrant parasites straying into new hosts are illustrated by him, mostly in connection with bacteria. An interesting series of illustrations from animal parasitology, such as the turkey gapeworm as a highly pathogenic "stray" in chickens, might have been added.

The fourth chapter, on the host-parasite conflict, brings together and discusses many facts and theories regarding immunity. The parasitologist will find in this chapter many ideas suggesting research along lines which have given some interesting results in bacteriology but which have been little tested and scarcely applied in animal parasitology. The offensive and defensive mechanisms of the parasite and the host are brought together, compared and discussed in succinct form.

In the fifth chapter, on cell parasitism and phagocytosis, the discussion of parasitism and of the host-parasite conflict is brought down to terms of cells. This chapter brings together such sub-

jects as cell fragility, functions of the reticulo-endothelial system, phagocytosis, allergy, bacteriotropin, opsonin, and antigen-antibody reactions in their relation to parasitology. From so many data and from such a confusing variety of points of view it would be difficult to conclude much in the present state of our knowledge. If Smith's summary in his final paragaraph is not very convincing or adequate, this is hardly ground for criticism when we consider the amount and the sometimes conflicting nature of the material he is attempting to digest.

The sixth chapter, on variation and mutation among parasites, emphasizes the plasticity of species and the importance of new variants among parasites, especially as pathogens. Here Smith is more at home in his discussion of bacteria than of animal parasites, and his statement that the human, bovine, porcine and canine whipworms may or may not represent four races would meet with the objection that whereas the human and porcine whipworms appear to be morphologically identical, the bovine and canine whipworms are definitely good species, quite distinct from each other and from the human-porcine form. His table on the decline of virulence in tubercle bacilli under cultivation appears to contain an error of some sort in the last item which shows the culture begun in 1932 and tested in 1931, a year before the culture was started. Smith doubts whether any free-living animals are now in process of becoming parasitic; the reviewer believes that evidence in regard to such forms as *Rhabditis strongyloides* justifies the suspicion that there are free-living forms which are developing parasitic habits at this time. Regardless of these things, the chapter, like other chapters, contains some very suggestive ideas for the parasitologist, and for students of heredity and variation.

The seventh chapter, on survival of parasites and movement from host to host, discusses the many ways by which parasites move from all sorts of positions in the host to new hosts, noting the need in some cases for breaking through host defences to accomplish this. The rôle of young host animals is discussed, and intrauterine infection considered. Such factors as antibodies, the effects of civilization, intermediate hosts, carriers, movements to unusual hosts, and multiple hosts are given interesting discussion.

The eighth chapter, on epidemiology, recounts the tale of several epidemic and endemic diseases of man and of the epizootic diseases of animals, and discusses these from the standpoint of parasitism. Smith's reason for regarding the mosquito as not an obligatory parasite is not the conventional reasoning of the parasitologist or in accord with conventional definition. He develops the value of research in the field of parasitology, in the wide sense of the word, in combating disease. This idea is finally given philosophic treatment in his concluding sentence: "The final suppression presupposes a world organization of human society without wars, and disarmed, such as the most pronounced idealist of today can scarcely conceive, but towards which human society must tend to survive in the struggle with animal and plant life, microscopic and ultramicroscopic." The reviewer concurs in the belief that if mankind is to survive it must fight its parasites and not itself.

The final chapter, on the utilization of discoveries in parasitism, opens with a protest against too much "purity" in science. "The objectives of research as a mere accumulation of data or the display and parading of acquired knowledge in a world otherwise in motion," he considers to be an outmoded concept. Discoveries, Smith says, must be made to yield some contribution to the welfare of mankind. Since parasitism is one of Nature's devices for cutting down life, it comes in conflict at some points with the dominance of the human race. In this chapter Smith presents parasitism largely from the philosophic angle. Humanity's defenses against parasites are summarized, with

a discussion of the current scientific theories regarding the mechanism of some of those defenses. Various forms of immunizing or of protecting against disease are given consideration as regards individuals and groups. Smith notes that as yet humanity has not completely wiped out even one infectious disease, thereby pointing out a goal which seems to the reviewer difficult enough and important enough to deserve consideration as one objective worthy the attention of mankind. With this thought the book is brought to a conclusion.

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✦

PATHOLOGICAL HEREDITY

ANY book which is the joint effort of a number of specialists in diverse fields is liable to gross abnormalities of development. These are evident as deficiencies, overgrowths, and lack of unity. When the scope of the several chapters has been determined and the work of writing them has been completed by the most competent men available, it then becomes the painful duty of the editor to unify the whole treatise by correcting deficiencies, lopping off overgrowths and even rewriting parts of the book if necessary. The Chances of Morbid Inheritance* left the press greatly in need of such editorial attention.

The book espouses the noble cause of bringing about coöperation of the medical profession in the collection of human genetic data, as well as the purpose of giving the medical man a text whereby he may arrive at a eugenical prognosis for patients desiring to know whether they ought to marry and procreate children. In plan the book devotes 449 pages to these purposes, and remains gracefully conservative in discussing the more common hereditary abnormalities of man. The book contains pedigree charts, but the almost complete absence of photographic illustrations will be greatly felt by the lay-reader and by many practitioners.

Sir Humphrey Rolleston says very aptly:

> There is some confusion in the public mind about the meaning of the word eugenics; many still regard it as connoting such measures as the compulsory mating of selected individuals on the lines of the methods employed in the stockyard, or the compulsory sterilization of those somewhat vaguely labelled unfit. To others, and among them members of the medical profession, the propaganda of eugenists appear to have outrun the existing knowledge of the laws of human heredity.

He complains that the better classes have adopted birth control methods, which are but little used by the "feckless and improvident." He states that "The aim of eugenics is to counteract this recent and racially harmful development of modern civilization."

R. R. Gates treats genetic principles in the usual fashion but refers the reader to his own book, *Heredity in Man*, for (p. 3) "the main facts with regard to the inheritance of normal and abnormal conditions in man, and also the results of racial crossing", (p. 7) "complications" which "have entered into the more recent investigations of eye-color inheritance in man", (p. 18) "albinism", and (p. 28) for mother-to-daughter pedigrees. In the opinion of the reviewer it is very unfortunate that the reader is made to feel that he must also procure a copy of *Heredity in Man* in order to learn the "main facts."

W. Russell Brain gives a fine account of the hereditary nervous disorders and, in a later chapter, epilepsy.

Aubrey Lewis discusses at length the difficulty of studying mental disorders from the hereditary standpoint, and gives

*BLACKER, C. B., M.C., M.A., M.D., M.R.C.P., General Secretary of the Eugenics Society (Editor), and SIR HUMPHREY ROLLESTON, Bart., G.C.V.O., K.C.B., M.D., D.Sc., LL.D., F.R.C.P., President of the Eugenics Society (Introduction). The Chances of Morbid Inheritance. Wm. Wood & Co., Baltimore, 1934.

special attention to manic depressive insanity, dementia praecox, paranoia, obsessional disorders, hysteria, senile and involutional types.

Henry Herd takes Goddard for an untimely "ride" on the subject of "unit-character" interpretation of mental deficiency. This might have been apropos a decade ago. Herd admits that heredity is an important factor in mental deficiency and says quite dogmatically that "the definitely defective should not marry."

Sir Stewart Duke-Elder modestly names the more common hereditary eye defects. He gives a list of literature but fails to mention the only comprehensive volume on the subject, that 631-page classic by Waardenburg.

R. J. Cann exposes the difficulties of studying the heredity of deafness, admits a certain hereditary tendency, but neglects to mention such a comprehensive analysis as that by Davenport, Milles and Frink on Otosclerosis.

George Bray treats the allergies, and finds that they are irregularly dominant, with individual variation in type of manifestation.

L. J. Witts gives a satisfying account of the diseases of the blood. Maurice Campbell discusses cardio-vascular conditions, A. Arnold Osman, the renal diseases. L. Forman treats diseases of the skin, but fails to mention the comprehensive volume of Cockayne in his literature references. Maurice Shaw discusses gastro-intestinal diseases, H. Gardiner Hill, the heredity of simple cretinism and toxemic goitre. R. D. Lawrence reviews diabetes mellitus and renal glycosuria.

E. R. Boland clowns through 24 pages. He is skeptical about the relationship of heredity to tuberculosis. He says, "The pioneer work of Villemin on the innoculability of tuberculosis and the discovery of the tubercle bacillus by Koch brought the whole edifice of medical tradition crashing down in ruins." Again, "By inherited susceptibility I mean . . . . the inheritance of a factor of susceptibility specific for the Tubercle bacillus, which could exist in a person living in a sphere where the Tubercle bacillus had no existence in the past, present, or future; a factor which seems as likely to exist as penny matchboxes in a world where matches are neither an abstract or concrete conception." Again, "Does long exposure to tubercular infection produce an immunity which is capable of being genetically transmitted? It appears very probable that this is the case, but there is little direct evidence" (Shades of Lamarck!). In a section labelled "Postscript" he quotes von Verschuer and Diehl's work to show that when one of a pair of monovular twins develops tuberculosis the other is more likely to develop the same disease than would be expected if heredity were not a contributing factor.

A. Piney appears to fight his chapter through its total length of five pages. He admits that von Recklinghausen's disease is hereditary. Of polyposis of the colon he says, "it is not clear whether we are dealing with the inheritance of neoplasia or only with the inheritance of a susceptibility to some unknown agent." "Nothing is commoner than to hear of cancer families, and few things are rarer than to meet with such an unfortunate collection of persons." (With the validity of so sweeping a statement some authorities would hardly agree!) Piney asserts that if glioma retinae patients live "only about 50% of the children will develop the disease. The method of inheritance is not clearly understood, but its occurrence presents good reason against procreation."

H. A. Harris gives a 25-page discourse on the sorts of developmental arrests which may take place, but becomes so engrossed with his subject that he does not get around to list the different inherited types of "Congenital Abnormalities of the Skeleton" which is his chapter title.

Lancelot Hogben adds instructions on how to analyse human data. After this follows a glossary of terms, the Eugenics Society's pedigree schedule and an index.

CLYDE E. KEELER
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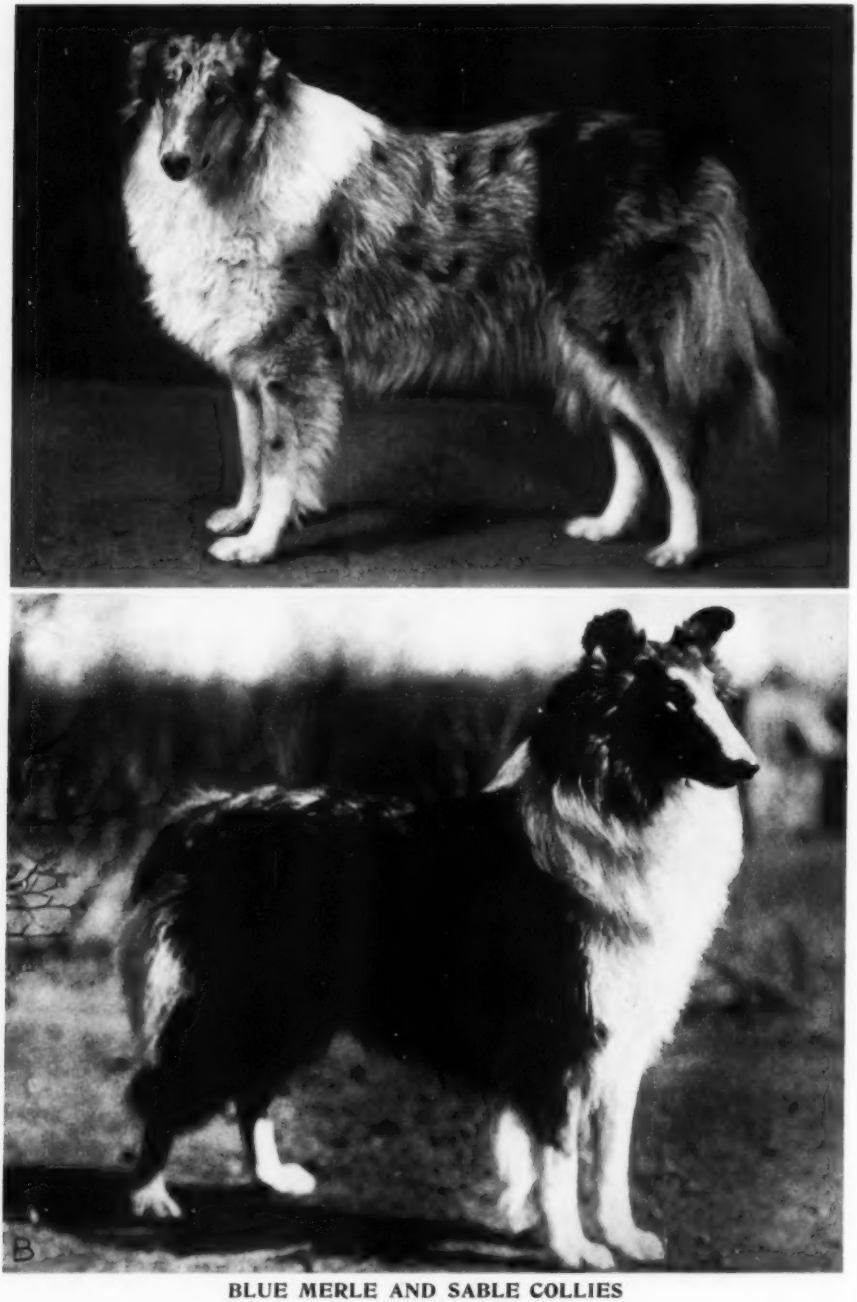

BLUE MERLE AND SABLE COLLIES

Figure 16

The Blue Merle Collie is another type depending on heterozygous genes, which is not in practice produced in a pure-breeding form. The merle pattern depends on a dominant dilution factor, *M*, which when homozygous (*MM*) results in blind and deaf individuals. Above is shown an outstanding blue merle bitch, Champion Heathbrae Bluebird, owned by Heathbrae Kennels (H. Spitler and A. Wolf). Her formula is $a^t a^t MmWWss$. Both eyes are dark and the expression is much better than is usually found in blue-merles. The Sable Collie shown below has the formula $A^y a^t mmWWss$ She was bred by the Arken Kennels (C. A. Wernsman) and later owned by the Royal Kennels (R. D. Bundy).

DOMINANT DILUTION AND OTHER COLOR FACTORS IN COLLIE DOGS

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WITH the cooperation and aid of a number of Collie breeders who have turned over to the author breeding records of undepleted litters, the inheritance of the blue-merle color in Collies has been determined. Pearson, Nettleship, and Usher[9] discussed this character of Collies in 1913 in their work on albinism in man, and a few years later both Wright[12] and Little[7] also mentioned it.

Practical Collie breeders have never completely understood this color, and some have even gone to the extent of doubting that the blue-merle color follows any definite law of heredity. When preliminary studies were commenced on blue-merle several years ago, it was found impossible to gain any worth while information from the American Kennel Club stud books. Further investigation led to the discovery that this most important color class was completely missing from the stud books, and was rarely mentioned even in the literature of the breed. The inclusion of this class in the records revealed quite clearly the manner in which the blue-merle color was inherited. It was found that this color was determined by a single semi-dominant unit gene which is, with rare exceptions, always found in the heterozygous state.

Collie Colors

Collies occur in the following colors: tricolor, blue-merle, sable and white, sable-merle, and white, as will be shown later in this paper. Since self colored Collies never occur, the breed must be in every case homozygous for the recessive white spotting in Collies described by Castle[2] in 1930, and which Little[7] designated in Great Danes as *s*. This spotting behaves as though subject to multiple modifying factors, for it ranges from low grade forms such as shown in Figure 17*A*, where white is present only on the chest, feet, and tail-tip, to the high grade forms in which there is a blaze extending over the head to meet a full wide collar which reaches back of the fore legs. In the highest grade form the white on the hind feet continues beyond the hock to meet the white underbody, and often the distal half of the tail is largely white. It is probable that the condition of two recessive allelomorphs causing white spotting, described by Castle[3] as occurring in Dutch rabbits, does not exist in Collies, although there is no evidence as yet to support that supposition.

The tricolor Collie is homozygous for the recessive bicolor black and tan factor described by Pocock[10], and by Barrows and Phillips[1]. This gene I shall designate as a^t. In addition, the usual white markings are present, so that tricolor Collies have the genetic formula a^ta^tss. In this breed the distribution of the tan areas is of the usual sort, the tan being limited to the sides of the muzzle, the cheeks, the chest, and inner margins of the legs. Figure 17 (*A* and *B*) shows good examples of tricolor Collies.

The blue-merle color is caused by the action of a single dominant gene for dilution, to which I shall assign the symbol *M*, upon the bicolor pattern. In the heterozygous condition the typical coloration consists of a blue-grey and slightly dilute tan ground color upon which are imposed irregular black blotches of different sizes. Figures 16*A* and 17*C* show typical specimens with blue-merle coloration. From this blotching or marling, the color gets its name. In addition the gene invades the eyes as well, causing usually a smoky grey eye which like the coat, has in it black blotches. This grey or "wall-eyed" condition is somewhat in disfavor with breeders of Collies who have found that by selection a dark eye can be bred in the blue merle. This is achieved by getting a black blotch to occur in the region of the iris, a process

which has been found to yield to selection. However, very often the result is an odd-eyed dog with one wall eye and one dark one, or else a dog with sectors of both colors in the same eye. In fact the odd-eyed condition is so common that a Collie of that type may win highest exhibition honors if it is an otherwise good specimen.

The homozygous condition (*MM*) of the merle factor creates a dog which is almost entirely white in appearance. These homozygotes may or may not have a few blue blotches here and there on the body, but in every case they are defective to some extent, although apparently not of impaired vigor. Color has been diluted to the vanishing point by the gene in duplex. The eyes are pale blue, almost china white and more or less sightless when present; and very often the homozygote is either unilaterally or bilaterally eyeless. Hearing is also affected and deafness is almost always complete. The skin, including the nose, foot pads, lips and eyelids are flesh-colored and pigmentless, except within the area of a blue spot. This type of Collie is usually destroyed at birth and practically never raised to maturity. In fact, some breeders will not admit that they are ever born in their kennels, although the heterozygotes are being constantly mated together.

At the present time I have a male Collie homozygous for the merle dilution factor which was saved and given to me as a puppy by the Tokalon Kennels. This Collie, which is pictured in Figure 18, is all white except for a blue area on the left side of the head which includes both the left eye and ear, a second spot on one side of the body and a third area covering the proximal half of the tail. His foot-pads and nails are white, his nose is part white and part blue. The left eye is light blue with a few spots of darker blue and has fair vision, although noticeably below normal. The other eye, however, is practically white and nearly sightless. For all practical purposes he is entirely deaf, and shows a negative reaction to the Galton whistle. There is thought to be some trace of hearing, however, as he is not mute but barks normally, and responds to occasional loud sounds. He is otherwise normal, quite intelligent, and a better than average specimen of the breed in physical conformation. In addition, breeding tests have shown him to be perfectly fertile.

Through the cooperation of Miss Elizabeth Whelan of Pocono kennels, Mrs. Bernice Unwin of Sunderland kennels, and a number of other Collie breeders, the author has collected the data in the following tables as well as other valuable information. The results of nine litters of Blue-merle by Blue-merle are given in Table I.

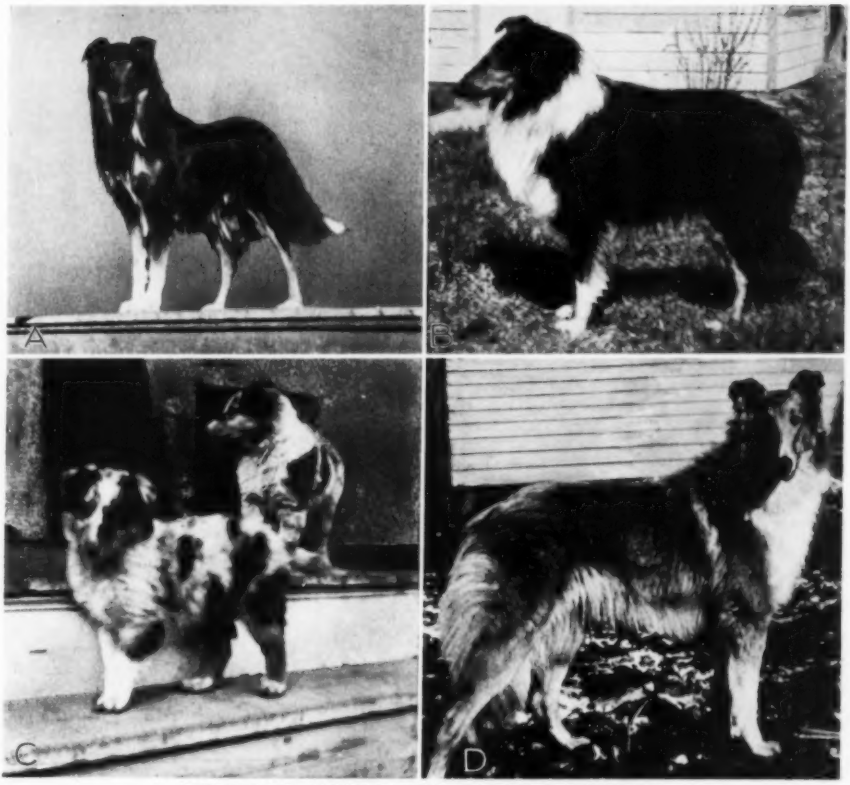
In Table I, the deviations in all three classes are constant, being only 0.01 times their respective probable errors. It can be seen that the observed data falls very closely into the expected 1:2:1 ratio, and shows clearly the semi-dominance of the factor *M*.

Blue-merle occurs in several other breeds besides the Collie, and with one or possibly two exceptions the color may be traced directly back to a point where these breeds were intermingled with the Collie. Those breeds other than the Collie, in which blue-merle occurs, are the Old English Sheepdog, Shetland Sheepdog, Great Dane, some of the Collie-like British herding dogs, and possibly the dappled Dachshund. The Old English Sheepdogs of today, at least as far as those in America are concerned, appear to be free of the factor (*M*), and owe their color to a different gene.

The Harlequin Pattern

Through the kindness of F. D. Kerr, a well known breeder of Great Danes, it has been found that the harlequin color in Danes is a modified form of the merle dilution factor (*M*), and is not a form of dominant piebald spotting as it has heretofore been considered.

The typical harlequin pattern in Great Danes consists of a white ground color upon which are imposed large black spots of irregular size and placement. This differs from the blue-merle coloration found in Collies in that the ground



TRICOLOR, MERLE AND SABLE PATTERNS

Figure 17

A—Black Beauty the Great, tricolor Collie owned by P. Hird. This is a very good example of the extreme low grade form of spotting sometimes found in Collies. His genetic formula is $a^t a^t mmlWWss$. B—Anahassitt Answer, tricolor Collie owned by Glenara Kennels. Note the distribution of the tan markings on head and legs. He has the same genetic formula as the preceding ($a^t a^t mmWWss$). *C*—Dark eyed blue-merle Collie puppies bred by Pocono Kennels (E. D. Whelen). These puppies show a considerable amount of black which is somewhat correlated with dark eyes. Their genetic formula is $a^t a^t MmWWss$. *D*—Pleasant Royal Lady of Arken, a good specimen of homozygous sable Collie, owned by the author. She has the genetic formula $A^y A^y mmWWss$.

color is white rather than blue or blue-grey. Apparently this difference is due to a single unit gene modifying the dominant dilution factor (M) to the extent of removal of all color from diluted areas. The dominance of this factor is uncertain, and the readiness with which the typical blue-merle coloration segregates from harlequin matings precludes any linkage between M and its modifier. According to Mr. Kerr, a blue-merle Dane is merely a badly colored harlequin, and matings of harlequin by harlequin produce harlequins, blue-merles, blacks, and all or nearly all-whites; the all-whites being deaf and dumb. He gave no figures or ratios of the proportions produced of each color class, but the data as presented agree with the present findings on blue-merle in collies. As Little and Jones[7] did not mention the occurrence of blue-merle in Danes in their study of

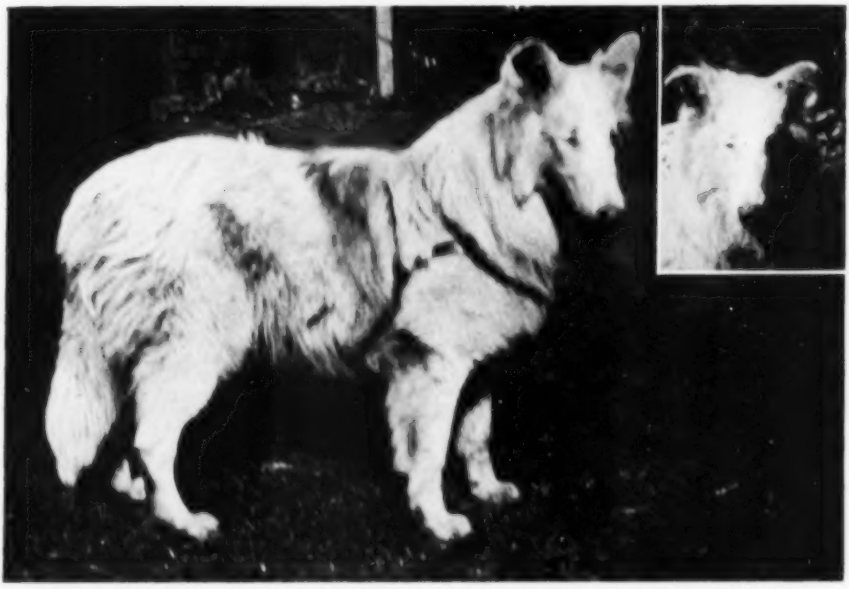
color in Great Danes, it is very likely that these are usually destroyed or at least not registered, and therefore do not appear in the American Kennel Club stud books. It is worthy of note that exhibition type harlequins often have blue spots mingled with the black spots on the white ground, and that the majority of living harlequins examined by myself have been of this type.

Sable and white is the commonest color found in Collies and has been described previously as a sort of sooty yellow by Wright[12]. Although sable Collies may be found in practically every shade of yellow, from very dark mahogany to pale straw color, the color is caused by a single dominant factor to which I shall assign the symbol A^y. The white on sable-and-white Collies is caused by the piebald character (ss) for which, as it was pointed out earlier, all Collies are homozygous. That sable (A^y) is allelomorphic to the recessive bicolor factor (a^t), is clearly shown in Table II, as well as in Tables III and IV under the discussion of sable-merle. Table II shows the results obtained by mating together the offspring of a mating between homozygous sable and tricolor.

In Table II, although the deviation is quite large, it is only 2.32 times the probable error. If a^t were not the allelomorph of A^y, a third class would appear that was neither sable nor tricolor, and a 12:3:1 ratio would be obtained. As Castle[1] includes bicolor (a^t) in the agouti series of the dog, sable (A^y) must of necessity also be a member of that series. This is the fourth agouti allelomorph to be recorded in dogs, the other two members of the series being according to Castle[2], agouti (A) and non agouti (a). When a sable Collie of the genetic constitution A^yA^y is mated with a dog homozygous for the agouti factor (AA), the offspring are all sable, as shown by several matings which I have observed between sable Collies and agouti (wolf grey) German Shepherd dogs. In all, 12 F_1's were observed, which represented one undepleted litter and two depleted ones. Since sable is dominant, sable and white Collies may be either of the genetic formula A^yA^y-*mmss* or A^ya^tmmss. Under this point rests the determination of what shade the sable Collie will be, since it has been observed in matings resulting in 44 litters that clear yellow sables are always found to breed true for A^y and can never produce tricolors, even when bred to a tricolor; Collies of the combination A^ya^t vary greatly in degree of darkness but are never a true clear yellow, although they may often closely approach it especially in their first adult coat. The variation shown in A^ya^t animals is apparently due to much the same sort of modifiers as those which cause sootiness in yellow house mice. In fact sable in Collies behaves much the same as dominant yellow in house mice except that in sable Collies adiposity is not present, nor is there any lethal action upon the homozygote. Homozygous sable Collies are as normal, and as vigorous as those of any other color, and are the most generally popular color bred in Collies. Figures 17*D* and 16*B* show good specimens of sable Collies.

Sable-merle is the term applied to Collies in which both the factor for sable and that for dominant dilution (M) occur. As M nearly always enters such a combination accompanied by a^t, the sable-merle usually has the formula A^ya^tMmss. The appearance of such a Collie is that of a light sable blotched with dark sable spots, and very often one or both eyes are either blue or contain blue sectors. Since the blotching is dark sable and not black, on a lighter sable ground, sable-merles often pass for ordinary sables either of the composition A^yA^y or A^ya^t unless blue shows in the eyes. Tables III and IV show the results obtained from matings of sable by blue-merle.

In Table III the first two classes were grouped together, since the contributors of the data made no distinction between sables and sable-merles. In both class one, and class two of Table III the deviation is greater than three times the probable error, being 3.75 times the probable error in class one, and 3.02 times the probable error in class two.



THE HOMOZYGOUS BLUE MERLE HAS DEFECTIVE EYES AND EARS

Figure 18

Toka of North Wind, a homozygous blue-merle ($a^t a^t MMWWss$). This Collie was bred by Tokalon Kennels and presented to the author. Breeders almost always destroy puppies of this type at birth. The insert shows a front view of his head. The right eye is nearly white and almost sightless while sight is nearly normal in the left eye which is light blue in color. This Collie is also deaf. He is otherwise the equal of the average Collie in physical conformation.

The deviation for class three was only 1.30 times the probable error. I do not consider these two large deviations to be significant since the deficiency occurs in two of the dominant classes, and the table is based on very small numbers.

Table IV was prepared on the basis of three litters totalling 25 individuals which had been accurately classified as being either sable or sable-merle. In this table the data fit the expected ratio very closely, the deviation being only 0.94 times the probable error. In addition to this there is the report of one breeder who mated a light sable to a blue-merle, and using the same pair of Collies produced over 50 F_1's, all of which were sables. This breeder, however, made no distinction between sable and sable-merle. When he mated one of the F_1 sable-merles back to the blue-merle, a litter was obtained which contained several puppies which were described as defective white puppies with tan spots. These would have the genetic formula $A^y a^t MMss$, and are evidence that the action of MM is just as strong in the presence of A^y as it is when it occurs combined with $a^t a^t$ in Collies or with aa in Danes. The only instance of a Collie of the genetic formula $A^y A^y Mmss$, was one produced from a sable-merle mated with a dark sable. This Collie was classified at birth as a blue-merle and was said to have "turned sable" as it became older.

White is a condition often met with in Collies, and is described by Harbert[4] as being due to a unit recessive gene which I shall call w. This factor has a spotting action resulting in the removal of color from the major portion of the body. These white Collies are perfectly normal and have dark eyes and points. As a

rule there is some color on the animal and the present fancy demands a Collie with a colored head and an entirely white body. Deafness is occasionally found in white Collies just as it is in some white breeds of dogs, white cats, and other white animals. The white factor (*w*) in Collies can occur in combination with sable and white, tricolor, or blue-merle, although it is but seldom bred with blue-merle, due to the inability of breeders to distinguish between white (*ww*) and homozygous merle (*MM*) individuals.

Summary

Coat color in Collies depends upon the interaction of three allelomorphic pairs of mendelizing factors, A^y, a^t; *M*, *m*; *W*, *w*; in addition, Collies are always homozygous for recessive piebald, *ss*.

Sable is caused by a dominant member of the agouti series, A^y, somewhat analogous to dominant yellow in mice.

Tricolor is caused by the factor a^t, the recessive allelomorph of A^y.

Blue-merle is the result of the dominant dilution factor, *M*, in the heterozygous state interacting with a^t. Dogs homozygous for *M*, are almost albinotic in appearance, always defective, and nearly always destroyed by the breeder soon after birth.

When A^y and *M* are combined, the resulting individual is termed a sable-merle, but does not differ greatly from sable unless blue appears in the eyes.

White occurs when the recessive factor, *w*, is present. This color is independent of A^y, a^t, *M*, or *m* and may occur in combination with any of them. Collies heterozygous for *w* often have somewhat larger and more prominent white markings than those free of the factor.

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Table I. Blue-merle x Blue-merle ($a^t a^t$ mmss x $a^t a^t$ mmss)

Class	White	Blue-merle	Tricolor
	$a^t a^t$ mmss	$a^t a^t$ Mmss	$a^t a^t$ mmss
Actual	80	39	80
Expected 1:2:1	19.75	39.25	19.75
Deviation / Probable error	0.01	0.01	0.01

Table II. Dark sable x Dark sable ($A^y A^y$ mmss x $A^y a^t$ mmss)

Class	Sable	Tricolor
	$A^y A^y$ mmss or $A^y a^t$ mmss	$a^t a^t$ mmss
Actual	14	9
Expected 3:1	17.25	5.75
Deviation / Probable error	2.38	2.38

Table III. Dark sable x Blue-merle ($A^y a^t$ mmss x $a^t a^t$ Mmss)

Class	Sable and Sable-merle	Blue-merle	Tricolor
	$A^y a^t$ mmss and $A^y a^t$ Mmss	$a^t a^t$ Mmss	$a^t a^t$ mmss
Actual	10	14	11
Expected 2:1:1 (1:1:1:1)	17.50	8.75	8.75
Deviation / Probable error	3.75	3.02	1.30

Table IV. Light sable x Blue-merle ($A^y A^y$ mmss x $a^t a^t$ Mmss)

Class	Sable	Sable-merle
	$A^y a^t$ mmss	$A^y a^t$ Mmss
Actual	14	11
Expected 1:1	12.50	12.50
Deviation / Probable error	0.94	0.94

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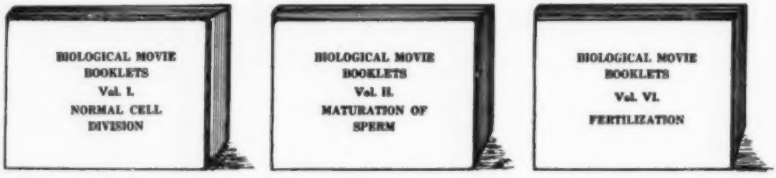

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